Volume LXXI Number 5

THE BOTANICAL GAZETTE

Editor: JOHN M. COULTER

MAY 1921

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THE BOTANICAL GAZETTE

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EDITED BY

JOHN M. COULTER

With the assistance of other members of the botanical staff of the University of Chicago

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MAY 1921

DORMANCY AND HARDINESS IN THE PLUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 280

P. D. STRAUSBAUGH

(WITH FOUR FIGURES)

It is a well known fact that the trees of our latitude develop buds during the period of vegetative activity, which remain inactive or dormant throughout the succeeding period of climatic conditions unfavorable for growth and development (ASKENASY 1). Although these dormant structures have been recognized for a long time, practically nothing is known concerning the factors involved in their development or the internal conditions that obtain during the time of their relative inactivity. Growth and development take place normally up to a certain point and then suddenly cease, in some instances several weeks earlier than the occurrence of temperatures sufficiently low to arrest growth activity. In late winter, the rest period is broken in many species, and growth changes are manifested long before the incipiency of warmer weather. Up to the present no specific experiments have dealt with the nature of the forces that induce cessation of growth in these bud structures, or the changes involved, either internal or external, in the resumption of the activity after a certain period of rest. The term "rest" as used here refers to a condition of greatly reduced, or possibly (for very short periods under certain conditions) a complete arrest of growth activity. Although no growth effects

are visible during dormancy, the metabolic processes are probably continued most of the time at a very greatly retarded rate.

In the plum there is a very definite relation between dormancy and hardiness or the ability to withstand low temperatures without suffering injury. Different species and varieties manifest widely differing degrees of dormancy, and in general the more profound the dormancy, the greater is the degree of hardiness. Furthermore, there is a close correlation in the plum between early maturity and deep dormancy, because those forms which show evidence of the earliest maturation in autumn are likewise the ones possessing the greatest degree of dormancy. This is a very significant relationship, for according to CHANDLER (4) maturity is "the most important factor affecting the hardiness of plant tissue."

Dormancy in seeds has been studied quite extensively, but little has been done to ascertain the nature of the dormancy that occurs in buds. The literature extant deals largely with the possible effects that external factors and forcing agents may have upon the rest period. SCHIMPER (10) maintains that "the protoplasm of the plants of temperate zones exists in two conditions, one active and one quiescent, and that the regular periodic alternation of these conditions is occasioned by inherent hereditary characters." HOWARD (6) asserts that "the rest sets in on account of the inhibition of enzymic activity due to over-accumulation of the products of their work." He holds that respiration and enzyme activity, continuing at a reduced rate, gradually remove the surplus of accumulated carbohydrates, and as a result the condition of dormancy is gradually lost. He further states that the fact "that the main dormant period happens to be coincident with the winter season is doubtless a mere coincidence, as the winter per se may, and probably does, have nothing to do with the beginning of the rest." This coincidence in all probability has a deeper significance than that which appears in this brief statement. Dormancy, whatever it involves, certainly represents an accumulation of tendencies which have been occasioned in the experience of the plant by marked changes in its environmental relations. Within the history of the plant kingdom striking temperature changes have occurred, and those forms which failed in the development of a

dormant condition, capable of resisting low temperatures, were eliminated from the field, and the forms which became dormant survived. Thus this coincidence is a direct result of adaptive reactions which have become a part of the heritage of the species. KLEBS (**8**) succeeded in preventing dormancy by controlling culture conditions, and MOLISCH (**9**) could break dormancy at will by subjecting the twigs to a water bath at high temperatures for a period of 10–12 hours.

While the knowledge of the external factors which affect dormancy gives a clearer comprehension of the phenomenon, an intensive chemical and physiological study of the changes in the bud at all stages in the growth cycle are required to discover the internal changes which parallel or precede the visible external changes. From such studies only can the facts be obtained which are essential to a full understanding of the changes that induce the rest period, the conditions that obtain during dormancy, or the initial changes in the resumption of growth.

Accordingly this investigation was begun with the object of determining some of the conditions which prevail in plum buds during the dormant period. Chief attention has been given to differences in the degree of dormancy in certain hardy and semi-hardy varieties, and to determining what relation (if any) might exist between the moisture content or moisture retention of dormant buds in different species and the relative resistance of these buds to low temperatures.

Material and methods

All the material used in this investigation was obtained from the University of Minnesota Fruit Breeding Farm at Zumbra Heights. Three varieties differing in hardiness were selected for study. The hardiest form, Assiniboine, is a variety of *Prunus nigra*, and has suffered little if any bud injury in Minnesota, even during the severest winters. Tonka is a cross between *P. triflora* var. Burbank and *P. americana* var. Wolf. The other variety, Stella, which has been used extensively, like Tonka, is a cross between *P. triflora* and *P. americana*. These two varieties differ markedly from Assiniboine in that during the most severe winters

as many as 50 per cent of the flower buds may be killed; consequently they may be placed in the semihardy group for a considerable portion of the state. The trees of each of these varieties from which material was obtained are about eight years old, and are growing in a dark, rich, silt loam soil. All are under clean cultivation without cover crops.

In making the moisture determinations, fruit buds were collected at the Fruit Breeding Farm in glass weighing dishes provided with closely fitted covers, at intervals varying from one to two weeks during the months from November 2 to March 31. On the evening of the same day the dishes containing the buds were brought into the laboratory, carefully weighed, and placed in an electric vacuum oven at 95°–98° C., with the pressure reduced to 8.5 cm. of mercury. The buds were kept in the oven until successive weighings indicated that all of the water had been removed from the tissues. In all determinations made before the middle of January it required about 72 hours to bring the buds to constant weight. After this date the desiccation began to take place more rapidly, and during the latter part of February the moisture could be completely evaporated in 24 hours. The extremely small size of the buds made it practically impossible to secure large samples for these determinations, since 200–250 buds were required for a single gram, wet weight. In the dehydration experiments the usual method was followed, in which the buds or twigs were placed in sealed chambers over sulphuric acid.

Relative degree of dormancy in hardy and semihardy forms

In determining differences in the degree of dormancy between the hardy and semihardy varieties, twigs were cut at intervals between October 3 and March 5 inclusive, and placed in water in the laboratory or greenhouse. In this way the fruit and flower buds were exposed to ordinary room temperatures, and careful notice was taken of all visible changes undergone, as well as the time required for anthesis. The results of these studies are shown in table I.

It is quite evident from these data that the buds of the semihardy varieties possess a very light dormancy, for when placed

under favorable conditions of temperature development proceeds normally, no matter at what stage of the dormant period the collection is made. On the other hand, the buds of Assiniboine collected before the middle of January are so deeply dormant that under the same conditions of temperature no visible change takes place and no blossoms are produced. Buds of Assiniboine, collected on January 24, bloomed 26 days later, on February 18. As this is the first visible response of these hardy buds, it is assumed to indicate the previous occurrence of some internal change which determines the breaking of the dormant condition. At this same

TABLE I

DEGREE OF DORMANCY OBTAINING IN HARDY AND SEMIHARDY BUDS AS MEASURED BY TIME REQUIRED FOR BLOOMING UNDER LABORATORY CONDITIONS AT DIFFERENT INTERVALS DURING SEASON OF DORMANCY

STELLA			TONKA			ASSINIBOINE		
Date of collection	Date of bloom	Time required for bloom	Date of collection	Date of bloom	Time required for bloom	Date of collection	Date of bloom	Time required for bloom
Oct. 3	Oct. 17	15	Oct. 3	Oct. 17	15	Oct. 3	.....	.....
Nov. 8	Nov. 22	15	Nov. 8	Nov. 22	15	Nov. 8	.....	.....
Nov. 19	Dec. 4	16	Nov. 19	Dec. 4	16	Nov. 19	.....	.....
Jan. 24	Feb. 2	10	Jan. 24	Feb. 2	10	Jan. 24	Feb. 18	26
Feb. 6	Feb. 15	10	Feb. 6	Feb. 15	10	Feb. 6	Feb. 23	18
Feb. 21	Mar. 2	11	Feb. 21	Mar. 2	11	Feb. 21	Mar. 8	17
Feb. 28	Mar. 7	9	Feb. 28	Mar. 7	9	Feb. 28	Mar. 14	16
Mar. 5	Mar. 13	9	Mar. 5	Mar. 13	9	Mar. 5	Mar. 19	15

time some change takes place also in the semihardy buds, for the period of development is shortened from 16 to 10 days. From January 24 throughout the remainder of the winter the degree of dormancy continues to decrease, and collections made on March 5 show that the length of time required for anthesis has been shortened to 9 days in the case of Stella and Tonka, and to 15 days in the case of Assiniboine. It must not be inferred that the time at which the break in dormancy occurs can be assigned to any particular day, for undoubtedly the changes involved proceed slowly, and development is initiated gradually. January 24 is emphasized as the time when the first evidence of a break in dormancy was observed, while in reality the changes involved may

extend through several weeks, taking place at a constantly accelerated rate as the season advances. It will be observed (figs. 1, 2) that the moisture content curve for Assiniboine shows some tendency

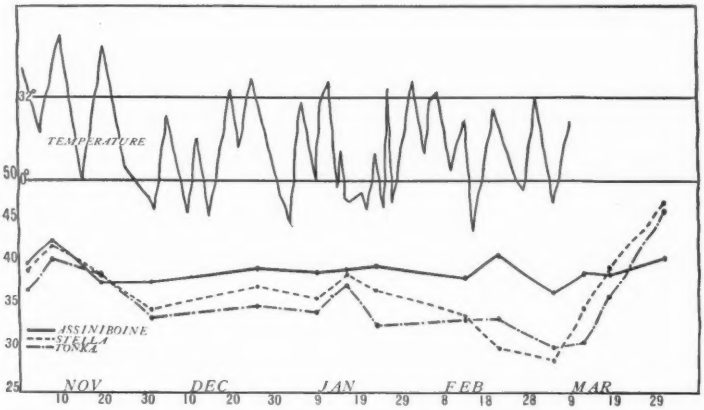

FIG. 1.—Moisture content fluctuations of leaf buds as related to temperature.

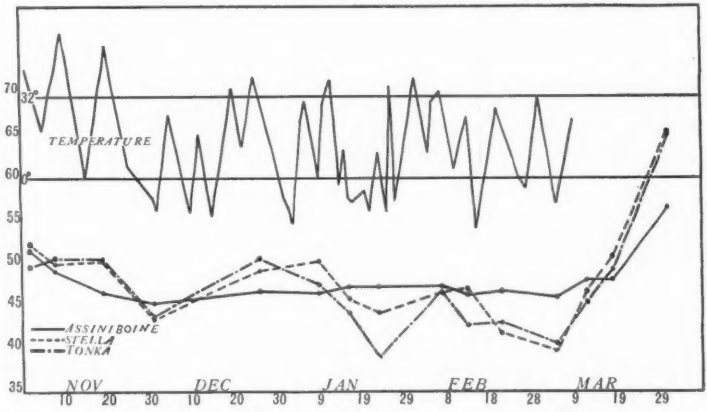

FIG. 2.—Moisture content fluctuations of fruit buds as related to temperature.

to become more irregular after January 25, and it may be that these fluctuations are due, in some measure at least, to internal changes incident to or causative of this break in dormancy. It is also significant to note here that the greatest injury to buds occurs

during the portion of the winter following this date, which marks an apparent (if not actual) break in dormancy (DORSEY and STRAUSBAUGH 5).

Moisture content and movement of water in hardy and semihardy buds

As in the break of dormancy, marked differences are also found in the moisture content of the hardy and semihardy buds. In both fruit and foliage buds of Assiniboine the moisture falls to a certain point early in the season, and then remains almost constant throughout the remainder of the winter up to the initiation of growth activity in the spring. In the buds of Stella and Tonka the moisture content undergoes some marked fluctuations during the course of the winter, and these coincide, in a general way at least, with corresponding fluctuations in temperature. The plotted

TABLE II

WATER LOSS FROM SEMIHARDY BUDS ACCOMPANYING MARKED LOWERING OF TEMPERATURES

VARIETY	FOLIAGE BUDS			FRUIT BUDS		
	November 19	December 1	Loss	November 19	December 1	Loss
Stella	39.08	34.68	4.40	50.38	43.51	6.87
Tonka	39.08	33.94	5.14	50.51	43.93	6.58
Assiniboine	38.12	38.30	.....	46.51	45.49	1.02

curves show three distinct periods at which such a behavior in water movement in relation to temperature is indicated, namely, on December 1, January 23, and March 5. On November 30 the temperature fell to 8° F., and on December 1 the thermometer registered −12° F. Bud collections made at this time showed a decrease in moisture content as indicated in table II.

From the data of this table it will be noted that while the moisture content of the foliage buds decreased 4.4 per cent and 5.14 per cent respectively in Stella and Tonka, the foliage buds of Assiniboine showed practically no change. In the case of the fruit buds the loss in Stella and Tonka is 6.87 per cent and 6.58 per cent, while those of Assiniboine show the very slight loss of 1.02 per cent.

On January 21 the temperature again fell to −12° F. and remained approximately at zero through the following day. Bud collections were made on January 23. The losses in moisture at this time are set forth in table III.

TABLE III

WATER LOSS FROM SEMIHARDY BUDS AS COMPARED WITH HARDY BUDS LATER IN THE SEASON

VARIETY	FOLIAGE BUDS			FRUIT BUDS		
	January 16	January 23	Loss	January 16	January 23	Loss
Stella	39.23	37.17	2.06	45.98	44.34	1.64
Tonka	37.83	33.13	4.70	44.41	39.16	5.25
Assiniboine	39.61	39.95	.....	47.36	47.31	0.05

In this instance it will be observed that the foliage buds in Stella and Tonka lose 2.06 per cent and 4.7 per cent respectively, while there is still practically no change in those of Assiniboine. Likewise the fruit buds in Stella and Tonka show a loss of 1.64 per cent and 5.25 per cent, while Assiniboine fruit buds show the almost inappreciable loss of 0.05 per cent. Again, on March 4, the temperature fell to 0° F. and on March 5 to −9° F. Bud collections made on March 5 showed losses in moisture content, as given in table IV.

TABLE IV

WATER LOSS FROM BUDS ACCOMPANYING MARKED LOWERING OF TEMPERATURE STILL LATER IN THE SEASON

VARIETY	FOLIAGE BUDS			FRUIT BUDS		
	February 21	March 5	Loss	February 21	March 5	Loss
Stella	30.25	28.87	1.38	41.98	39.78	2.20
Tonka	33.82	30.22	3.60	43.24	40.46	2.78
Assiniboine	41.20	36.87	4.33	46.83	46.16	0.67

On this date the moisture content of foliage buds in Stella decreased 1.38 per cent and in Tonka 3.6 per cent. The foliage buds of Assiniboine here show a loss of 4.33 per cent, which is not in accord with the data shown in tables II and III. This high percentage, however, is undoubtedly due to some error in the determination of moisture content for February 21, the value

(41.20 per cent) obtained on this date being too high to agree with the general results of the other determinations. The fruit buds of Stella and Tonka show losses of 2.2 per cent and 2.78 per cent, while those of Assiniboine show a loss of only 0.67 per cent. The changes in moisture content as shown in tables III and IV are not so great as those observed in table II. The curves (figs. 1, 2) show this relation much more clearly. It would have been interesting, for the sake of comparison, to have made determinations on February 15, when the lowest temperature of the winter was reached, but unfortunately no collections were made between February 13 and February 21.

TABLE V

INCREASE IN WATER CONTENT OF SEMIHARDY BUDS ACCOMPANYING MARKED RISE IN TEMPERATURE

VARIETY	FOLIAGE BUDS			FRUIT BUDS		
	December 1	December 26	Increase	December 1	December 26	Increase
Stella	34.68	37.6	2.92	43.51	49.3	5.79
Tonka	33.94	35.2	1.26	43.93	50.7	6.77
Assiniboine	38.30	39.7	1.40	45.94	46.80	0.86

It will now be interesting to note what effect a marked rise in temperature will have upon the water content. The temperature from December 20 to December 26 was relatively high, ranging well over 20° throughout this time and reaching a maximum of 40°. Bud collection made on December 25 showed a moisture content as given in table V. In this table it appears that the moisture content under certain conditions may increase with rise in temperature. Foliage buds of Stella showed an increase of 2.92 per cent, those of Tonka 1.26 per cent, while those of Assiniboine showed an increase of 1.4 per cent. In comparison with the foliage buds, the fruit buds of Stella and Tonka increased their moisture content 5.79 per cent and 6.77 per cent respectively; and in contrast the fruit buds of Assiniboine showed a strikingly slight increase of only 0.86 per cent. Thus it seems evident that the movement of water in the semihardy twigs and buds is easily influenced by fluctuations in temperature, but the response in

hardy buds to the same conditions is more tardy and much less pronounced. In March when the buds begin to swell the moisture content increases very rapidly, as is shown in table VI.

Table VI shows clearly the slower movement of water in the hardy form, for while the moisture content in the foliage buds of the

TABLE VI

INCREASE IN WATER CONTENT WHEN BUDS ARE RESUMING GROWTH ACTIVITY IN SPRING

VARIETY	FOLIAGE BUDS			FRUIT BUDS		
	March 5	March 31	Increase	March 5	March 31	Increase
Stella	28.87	47.28	18.41	39.78	65.58	25.80
Tonka	30.22	46.27	16.05	40.46	65.37	24.91
Assiniboine	36.87	40.70	3.83	46.16	56.52	10.36

TABLE VII

SUMMARY OF DATA ON MOISTURE CONTENT OF LEAF AND FRUIT BUDS FOR NOVEMBER 8 TO MARCH 31

DATE	TONKA		STELLA		ASSINIBOINE	
	Leaf bud	Fruit bud	Leaf bud	Fruit bud	Leaf bud	Fruit bud
November 8	40.57	50.64	42.34	50.01	43.15	49.38
November 19	39.08	50.51	39.08	50.38	38.12	46.51
December 1	33.94	43.93	34.68	43.51	38.30	45.49
December 26	35.2	50.7	37.6	49.3	39.7	46.8
January 9	34.4	47.5	36.0	50.3	39.03	46.6
January 16	37.83	44.41	39.23	45.98	39.61	47.36
January 23	33.13	39.16	37.17	44.34	39.95	47.31
February 6	.....	46.55(?)	34.29	46.54	.....	47.43
February 13	33.74	42.89	34.14	47.17	38.64	46.44
February 21	33.82	43.24	30.25	41.98	41.20	46.83
March 6	30.22	40.46	28.87	39.78	36.87	46.16
March 12	30.83	45.51	34.83	46.75	39.37	48.12
March 18	36.20	49.43	39.71	50.93	39.03	48.04
March 31	46.27	65.37	47.28	65.58	40.70	56.52

semihardy varieties increased 18.41 per cent and 16.05 per cent, that of the hardy Assiniboine increased only 3.83 per cent. In the fruit buds of Stella and Tonka the increase was 25.8 per cent and 24.91 per cent, while that of Assiniboine was only 10.36 per cent. It will be seen that marked and well defined changes take place in the water content of buds under different sets of conditions.

These changes appear conspicuously when the data for the entire dormant season are presented.

An examination of the data of Table VII reveals three very significant facts. First it will be noticed that throughout the period of dormancy the moisture content of the leaf buds of a given variety is considerably lower than that of the fruit buds. This may be a factor in the greater resistance of the leaf buds to low temperatures. In the second place it will be observed that the moisture content of the leaf buds of Assiniboine is uniformly higher than that of the leaf buds of the other two varieties. Lastly the moisture content of the fruit buds of Assiniboine is lower or higher than that of the fruit buds of Stella and Tonka according to the temperatures prevailing at the time the collections are made.

Dehydration of buds by sulphuric acid

When the marked differences in moisture content and moisture retention of leaf and fruit buds in these varieties with different degrees of hardiness became apparent, it seemed advisable to investigate such differences further. Accordingly a series of experiments was undertaken, first with buds alone, and later with buds attached to the twigs, to study the movement of moisture by carefully controlled laboratory methods. Fruit buds were collected in small weighing dishes provided with closely fitting covers. These dishes were then placed uncovered in sealed chambers containing different concentrations of sulphuric acid. The buds were weighed before being placed in the chambers, and subsequently at intervals of 12–48 hours, to determine the water loss. When the weighings were being made the lids were placed on the dishes while they were out of the chambers.

The results of the experiment with buds alone were not entirely satisfactory, and consequently it was repeated with one very essential modification, namely, the fruit and flower buds were not detached from the twigs. In the repetition experiment entire twigs 10–12 inches in length, with buds attached, were removed from the tree and placed in sealed chambers so that the twig-bud system as a unit was exposed to the air inclosed over different concentrations of sulphuric acid. In determining the moisture losses

weighings were made as before. The desiccators in these experiments were kept in a refrigeration room where the temperature remained quite constant at about 34° F. This low temperature

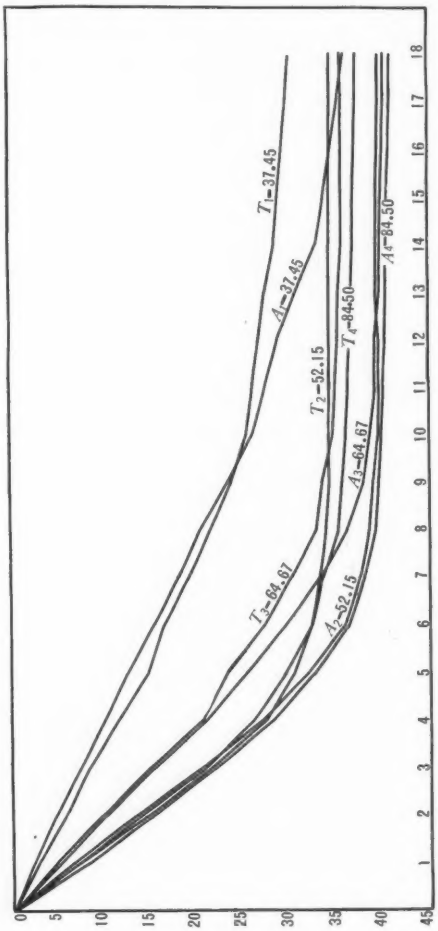

FIG. 3.—Loss of moisture from detached buds exposed to an atmosphere inclosed over sulphuric acid of different concentrations; *A*, Assiniboine; *T*, Tonka; numbers indicate concentration of acids; *C*, distilled water check.

was chosen as a precautionary measure against the possibility of the occurrence of any growth changes. Fig. 3 shows that the loss is almost uniform in both hardy and semihardy buds in every case

except those in which the more dilute acids were used. Since this uniformity of water movement in both hardy and semihardy buds was not in accord with the behavior of the buds under normal conditions, it was thought that it might be due to the escape of

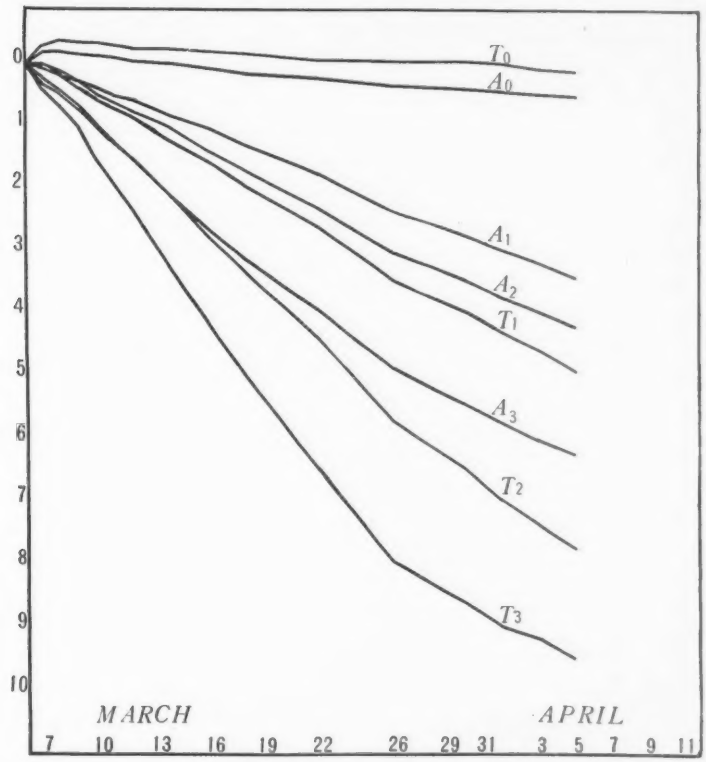

FIG. 4.—Loss of moisture from twigs with buds attached when exposed to atmosphere inclosed over sulphuric acid of different concentrations; *A*, Assiniboine; *T*, Tonka; concentrations of acid as follows: (1) 24.12 per cent, (2) 37.45 per cent, and (3) 84.50 per cent; *C*, distilled water check.

moisture through the wound surface made in severing the buds from the twigs. To test this assumption a collection of twigs with the buds in place was introduced into the sealed chambers and weighed at regular intervals of 24–48 hours. The cut ends of the

twigs were sealed with paraffin immediately after they were removed from the tree, so that all escape of water from the tissues must have taken place in a manner similar to that which occurs under normal conditions when the twigs remain on the tree. Fig. 4 and table VIII show the results of this experiment.

TABLE VIII

PERCENTAGE OF MOISTURE LOST FROM TWIGS OF TONKA AND ASSINIBOINE WHEN EXPOSED TO AN ATMOSPHERE OVER DIFFERENT CONCENTRATIONS OF SULPHURIC ACID FOR 28 DAYS

Variety	Percentage loss over distilled water	Percentage loss over H_2SO_4 (24.12%)	Percentage loss over H_2SO_4 (37.45%)	Percentage loss over H_2SO_4 (84.50%)
Tonka	0.04	4.83	7.7	9.49
Assiniboine	0.48	3.38	4.17	6.2

It will be noted that the water loss from the semihardy twigs is much greater than from the hardy twigs. With the highest concentration of acid used, the loss from the semihardy twigs is nearly 9.5 per cent, while that from the hardy twigs is slightly over 6 per cent. This tardiness in water movement is in full agreement with that occurring in the twigs under normal conditions as shown in the graphs of the moisture content curves. It will also be observed (fig. 4) that the twigs exposed to a saturated atmosphere over distilled water absorbed less than 0.5 per cent of moisture. This fact would seem to counter the claims of some workers to the effect that there is a considerable exchange of moisture between the tissues and the air, and to establish beyond doubt that the moisture content of the twigs does not increase markedly with an increase in atmospheric humidity.

In order to determine the relative amounts of moisture given off from the twigs to the air through evaporation caused by winds, twigs of four varieties, including hardy and semihardy forms, were removed from the trees and the cut ends immediately sealed with paraffin. These twigs were then supported upright in Petri dishes by means of paraffin, and after being weighed were placed in a strong current of air produced by two large electric fans. The dishes containing the twigs were weighed daily, and at the end of

three days the loss in all cases was found to be practically negligible, the greatest loss being only 0.7 gm. from a total weight of 137.47 gm., or a little more than 0.5 per cent. Thus it seems quite evident that there is little exchange of moisture between the air and the tissues of the twigs due to evaporation alone, but that some dehydrating force is necessary to account for such losses as have been shown to take place in connection with low temperatures.

In the studies of water loss from twigs in the acid chambers and also by the fan method, a conspicuous structural difference in the bark of the hardy form as compared with that of semihardy forms became evident. This difference may possibly be associated in some way with the slower movement of water in the hardy variety. The twigs in all three of the forms studied are covered with a heavy suberized layer which renders them impervious to water except through the lenticels. The number of these lenticels per unit surface is fairly constant for a given variety, but a marked difference is observed between hardy and semihardy varieties. Five separate counts were made on sections of twigs of Stella and Assiniboine. The sections chosen were 5 cm. long and 1.2 cm. in diameter, representing in each case a curved surface area of 18.85 sq. cm. Table IX gives the result of these counts.

TABLE IX

NUMBER OF LENTICELS PRESENT ON 18.85 SQ. CM. OF TWIG SURFACE

STELLA	ASSINIBOINE
49	12
54	10
48	8
39	13
54	11

As these lenticels are approximately the same size in each variety, it will be seen that the total lenticel area in the semihardy form is from 3 to 6 times that occurring in the hardy variety. The exact significance of this marked difference in bark character is not fully clear, but that it may be related in some way to the more tardy movement of water from the twigs of Assiniboine is a possibility that seems worthy of consideration.

Discussion

In recent years the horticulturists of the northern United States and Canada have been greatly interested in the breeding of hardy fruits capable of resisting the low temperatures of this latitude. One of the difficulties met with in this work has been the amount of time required to test new seedlings for hardiness. Various attempts have been made to discover some means of detecting hardiness by direct observation at an early period in the development of the seedling.

BEACH and ALLEN (3) made a rather extensive series of microscopical, mechanical, and specific gravity tests of apple twigs to ascertain whether "the hardiness of a tree could be determined while it was still in the nursery." They concluded that "from the practical point of view as yet it is impossible to name any one test by which the degree of constitutional hardiness of a seedling apple may be foretold." This work, however, has revealed some very interesting and suggestive facts that may have a fundamental value in the physiological study of hardiness. Among other things they found that "the hardier varieties on the average had a slightly lower moisture content than the more tender varieties," and that "this difference is more marked during the growing season." They state that this "difference in water content can be explained partly at least by the fact that the more tender sorts evaporate water more rapidly than do the hardy varieties. Freezing tends to dry the twig out, and after a period of very cold weather the twigs of the hardy varieties are generally found to contain the most moisture."

JOHNSTON (7) found that "as the season advances the difference between the water content of fruit buds of the Elberta and Greensboro peach becomes more marked, the values for the Elberta being the greater." Since the Greensboro peach is considered more hardy than the Elberta, the inference is that the more tender buds have the highest moisture content. In these determinations only 10 buds were used in a sample, and it would seem that larger amounts of the tissue might give more reliable results.

SHUTT (11) found the moisture content of apple twigs of tender varieties higher than that of hardy twigs. He stated "that we have

direct and definite proof that there is distinct relationship between the moisture content of the twig and its power to resist the action of frost, and that those trees whose new growth contains the largest percentage of water as winter approaches are in all probability the most tender." He also believes that hardiness is a quality that can be affected by cultural methods. He says that "hardiness is evidently something more than an inherited tendency. It seems probable that it is a quality largely under the influence of the soil conditions as regards moisture and temperature in the late summer and autumn months, and probably these factors rather than the severity of the succeeding winter determine the tree's immunity from frost. If in northern latitudes vegetative growth be early arrested and ripening of the new wood thus induced, either by artificial means (pruning and cover crops) or by a dry and cold autumn, varieties now considered tender might prove hardy."

There can be no doubt as to the effect of cultural methods upon the ability of certain plants to withstand low temperatures. This effect is shown by the work of BATCHELOR and REED (2), who found that one of the factors in the winter injury of the Persian walnut (*Juglans regia*) was winter drought. The injury referred to is a killing of the distal ends of the branches rather than that of the buds alone. Under certain conditions they were able to prevent winter injury by irrigating heavily late in the season, after maturation had been induced by withholding the water supply during the latter part of the summer. Their work shows a very evident relation between soil moisture and winter injury.

In the introduction attention was called to the fact that dormancy occurs in widely varying degrees. The range extends from no dormancy at all to profound dormancy, with every degree of intergrading conditions. If in perennial woody plants there is a positive correlation between dormancy and hardiness, it follows that there must be a corresponding range of hardy conditions. If the forms under consideration chance to be closely related as to position in the series, or closely adjusted to the equilibrium of the external environment, it is easily conceivable that cultural methods may affect the relative degree of hardiness within certain limits. Such a case would seem to be exemplified by the Persian walnut

grown under California conditions. On the other hand, it must be admitted that other factors are operating when we have to deal with forms whose requirements lie well within the limits of physical environment, or with forms widely separated in respect to the degree of hardiness they possess. It is difficult to conceive of any modification of external conditions that could induce a degree of hardiness in Tonka and Stella which would even approach the hardy condition that obtains in Assiniboine. The fact should be kept in mind, however, that Assiniboine belongs to a different species from Stella and Tonka, and also that what is true of the apple need not of necessity be true of the plum or the peach.

The investigations show a higher moisture content for tender apple twigs and tender peach buds than that of the hardier forms. In the plum, however, at least during the period of dormancy, it is not the relative amount of water present in the buds, but the relative water-retaining capacity that constitutes a distinct difference between hardy and semihardy forms. In the apple, BEACH and ALLEN found that the greater moisture content of the tender twigs as compared with hardy twigs was much more pronounced during the growing season. Whether such a relation obtains between hardy and tender varieties of the plum during the period of vegetative activity has not yet been determined. It may easily be possible that the problem of hardiness will require specific investigation for each species in question, and that as yet no very far reaching generalizations on the subject can be made.

In the case of the plum, microchemical studies (5) indicate that the dormant condition of the buds involves a protoplasmic change of some sort which is much more marked in the buds of the hardy variety. There is an evident modification in the proteins of the buds, but practically nothing is known at present concerning the nature of this change. It is possible that there is induced as a result of these modifications a very decided change in the colloidal condition within the cells which increases the force of imbibition, so that the water of the protoplast is retained against the dehydrating force of freezing, and the protoplasm is not disorganized. There is no evidence that the hardy buds contain less moisture than the tender buds during the dormant period; in fact, when the temperature drops very low the hardy buds contain the most water

(figs. 1, 2 and table VII). The point that must be emphasized, however, is that the hardy buds have the capacity to retain their moisture at a certain definite and fairly constant minimum throughout the period of dormancy regardless of all fluctuations in temperature, and that this capacity is not a characteristic of the semihardy or tender buds. WIEGAND (12) states as follows:

> Every cell has its critical point, the withdrawal of water beyond which will cause the death of the cell, whether by ordinary evaporation or by other means. It may be supposed that the delicate structure of the protoplasm necessary to constitute living matter can no longer sustain itself when too many molecules of water are removed from its support. In the great majority of plants this point lies so high in the water content that it is passed very soon after the inception of ice formation, hence the death of so many plants at this period. Others may be able to exist with so little water that a very low temperature is necessary before a sufficient quantity is abstracted to cause death. From some plants enough water cannot be extracted by cold to kill them.

The hardy plum, Assiniboine, lies very close to the last mentioned class of plants. It requires exceedingly low temperatures to cause it injury, and the explanation of this fact seems to lie in its ability to retain its moisture. Water movement in its tissues seems to be much slower, so that it matures earlier in the autumn and assumes its maximum water content more slowly in the spring. The fact that it blooms from two to three days earlier than the semihardy varieties may be due to the possibility of growth activities taking place with a much lower water content.

The moisture relations that obtain between the hardy and semihardy buds of the plum indicate a wide difference in their physiological reactions. These reactions arise from specific conditions within the cells, and therefore it is assumed that the protoplasmic structure of the hardy tissues is different from that of the semihardy tissues. These differences are inherent, so that they furnish a basis for the work of the plant breeder. There is a suggestion here, therefore, that a study of the moisture relations of seedling plants during both the dormant and vegetative conditions may afford a tentative basis for determining selections.

Summary

1. In the plum there are widely differing degrees of dormancy among the different species and varieties. There appears to be a

definite relation between dormancy and hardiness. Assiniboine is extremely hardy and its dormancy is very profound, in contrast with Tonka and Stella, two semihardy varieties in Minnesota, which appear to enter real dormancy for only a very short period in early winter, if they do so at all.

2. During the period of dormancy the moisture content of the semihardy varieties fluctuates with the temperature. Periods of low temperatures are accompanied by a loss of moisture from the leaf and fruit buds, and higher winter temperatures, which are seldom above freezing in Minnesota, by an increase in moisture content. In comparison with the semihardy varieties the moisture content of Assiniboine remains at a definite and fairly constant minimum throughout dormancy.

3. When the fluctuations in the moisture content of buds were found to occur under orchard conditions, this phase of the problem was checked under control in the laboratory by placing the twig-bud-system in sealed chambers over different concentrations of sulphuric acid. By this method water movement in the tissues of Assiniboine was found to take place more slowly than in Stella and Tonka. Lenticel number per unit area was found to be correlated with the difference in moisture retaining capacity.

4. Somewhere near the mid-point of the dormant period fundamental metabolic changes occur which affect the ecological reactions of apparently dormant plum trees in a striking manner. As a result of these changes, or at least coincident with them, winter killing in the flower buds is found for the first time, the moisture retaining capacity of the fruit and leaf buds is changed, and anthesis occurs when fruit buds are subjected to favorable growth temperatures in the greenhouse. These changes are interpreted as indicating the time when the rest period is broken.

5. The dormant condition reached by the hardy forms, such as Assiniboine, appears to involve fundamental protoplasmic changes. Among these there may be a change in colloidal properties creating an increased imbibition which may account for the marked retention of water against the force of dehydration.

6. This investigation has a direct bearing upon the applied problem of selecting seedling fruits for hardiness. A study of the

moisture relations in forms differing in hardiness may furnish the fruit breeder with a criterion, correlated with hardiness, which will hasten markedly the final selections.

This investigation was carried on in the laboratory of Dr. M. J. DORSEY, in charge of the Section of Fruit Breeding, Department of Horticulture, University of Minnesota. The writer is very grateful for all the favors accorded him, and especially for the constant aid and valuable suggestions received from Dr. DORSEY. I also wish to acknowledge the helpful criticism and advice given by Dr. SOPHIA H. ECKERSON, Dr. WILLIAM CROCKER, Dr. J. J. WILLAMAN, and Dr. L. I. KNIGHT. I am also greatly indebted to Messrs J. W. BUSHNELL, J. H. BEAUMONT, and A. C. HILDRETH for assistance in collecting material and data.

COLLEGE OF WOOSTER
WOOSTER, OHIO

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EVOLUTION OF ZOOCECIDIA

B. W. WELLS

(WITH PLATES XXI, XXII)

The basic conceptions back of the present treatment of the zoocecidial problem are those connoted by the word evolution. For some time the idea that galls have had their phylogeny along with other organisms and parts of organisms has occupied a prominent place in the mind of the writer. Definite attention to this phase of the zoocecidial problem has resulted in the development of outlines of the probable evolution in the various gall groups. This paper is an attempt to give in outline merely the phylogeny of zoocecidia, based in lesser part on embryological data, in greater part on comparative morphological material. Paleontological research has brought so few forms to light that no assistance can be gained from that source. A discussion of the conceptions which are basic for such a treatment of zoocecidia is also given, together with the elucidation of a new interpretation pertaining to the relation of the lower and higher galls.

Historical

In very few papers dealing with the comparative morphological aspects of galls has any attention been devoted to phylogenetic problems; the emphasis has been on the delineation of anatomical detail. No definite studies from a strictly phylogenetic point of view seem to have been made by Europeans. KÜSTER'S recent and extensive studies (**9**, **10**) do not include this point of view, at least not as gall phylogeny is interpreted by the writer.

At the outset careful distinction must be made between conceptions which are basic for the development of phylogenetic outlines and the phylogenetic outlines or "trees" themselves. Historically two interpretations which are basic for the development of zoocecidial phylogenies are extant: (1) gall characters are merely the reappearance of the host plant characters, either those immediately present or those hypothetically latent in the germ

plasm (meristem); (2) gall characters are the result of the influence of both the plant and the animal, chiefly the plant in the lower galls and chiefly the animal in the higher galls. In connection with the first interpretation, KÜSTER (10) expresses his astonishment at the multiplicity of the possibilities possessed by the cells composing the leaves. This consideration of the exceptional normal forms does not enable him to foresee this multiplicity, and throughout his writings there is the same emphasis. The plant cells are loaded with reaction possibilities, due, as KÜSTER intimates, to the retention of an array of latent characters acquired in the course of evolution. His example of the *Adelges* gall on spruce as being similar to the normal cone of *Sciadopitys* is a case in point.

COSENS and SINCLAIR (4), in a study of certain willow galls, present a similar interpretation. They say "The reinstatement in a gall of vestigial characteristics of the plant has an important bearing on the question of gall formation." They recognize, however, "a directive control over the activities of the protoplasm of the host" on the part of the cecidozoon, the result of which is referred to as an "environmental modification." The force of this recognition is weakened by their final statement that "there remains no authentic instance of any organ or tissue in a gall that is new, ontogenetically or phylogenetically, to the host."

With regard to the second interpretation, although a number of European writers, ADLER, FOCKEU, and others, have recognized the essential "independence" of the higher galls (prosoplasmas of KÜSTER), they have not gone so far as to formulate any definite conceptions of gall phylogeny; only the recognition of the fact that certain galls show characters which could not possibly have sprung from the plant has been given.

For the introduction of some genuine phylogenetic theories we must refer to COOK'S (2) study, which gives such statements as the following:

> The morphological character of the gall depends upon the genus of the insect producing it rather than upon the plant on which it is produced. The families show parallel lines of development from a low form up to a high form. The Acarin may be considered the lowest group of galls, the Aphidid the next higher, the Cecidomyia galls the next higher, and the Cynipidous galls the highest. However, many of the Cynipidous galls are lower than the Aphidid galls.

Thus COOK, in his recognition of the correlation between the taxonomic position of the gall-making animal groups and the degree of complexity of the galls produced by them respectively, has laid, in part, the foundation for the present discussion. In COOK's papers, however, anatomy and etiology are his major concern. Only in the instance of a few cynipid galls did he present the probable phylogenetic relationships.

Basic data involved in phylogenies

BEYERINCK (1), in his primary division of galls into those characterized by indefinite growth and those exhibiting definite growth, made an initial contribution of great significance. KÜSTER amplified this conception into the following two groups: (1) Kataplasmas; all those galls which are characterized by inconstancy and indefiniteness with regard to size and tissue form characters; there is also associated an indefinite time element; they invariably fall below corresponding normal parts in their differentiation, and what differentiation does ensue shows no new fundamental orientation of tissues as contrasted with the normal arrangement; (2) Prosoplasmas; all those galls which are characterized by definite size, tissue form, and time of development; in their differentiation they are not so much below the normal as they are different from the normal; in their form characters and orientation of tissues they are fundamentally different from the normal; they may be different in other characters as well, such as quality and quantity of organic substances contained.

KÜSTER (**9, 10**) has a preliminary division, his so-called "organoide and histoide" groups. Since the first, consisting of very slight modifications of normal organs, can be interpreted as very primitive kataplasmas, there is no significance to this classification; in the opinion of the writer it may well be discounted.

Major phylogenetic factors

1. THE PLANT.—The influence of the plant and its evolution are most strikingly observed in the kataplasmas, since these structures are for the most part not very far removed in their constitution from the condition obtaining in the normal plant. They

vary from the simplest type in which there is but a slight inhibition of differentiation, to the advanced condition in which differentiation is practically inhibited, only a mass of homogeneous tissue resulting. In the prosoplasmas the contribution of the plant is practically confined to the furnishing of cell types merely, and not differentiation and tissue form conditions.

2. THE ADULT CECIDOZOON (IMAGO).—(*a*) *Structural aspects.*—In the lowest cecidozoons, Rotifera, Copepoda, Nematoda, and Acarina, the adult stages as well as the larval stages are concerned in gall-making. With some unimportant exceptions in the Acarina galls, the cecidia are all kataplasmas. Above these groups we have but one genus in which the adult is concerned in definite gall formation, the genus *Pontania* of the Tenthredinidae (saw flies). The terebra's mechanical injury plus the introduction of a specific liquid substance results in a kataplasma of an advanced type, for the lack of differentiated tissues is a striking characteristic of these galls. The prevailing condition among insect cecidozoons, however, is that in which the larval stages only are concerned in gall formation. This is invariably true if the galls are prosoplasmas.

(*b*) *Behavior aspects.*—Throughout all gall-making groups the instinctive behavior of the adults is a factor with regard to resultant gall conditions. Choice of plant part attacked, number of eggs laid at one point, time of attack, all have something to do with resultant characters. From the standpoint of the fundamental nature and specificity of the individual gall, however, these behavior aspects play but a very minor rôle.

3. THE LARVAL CECIDOZOON.—In the larval cecidozoon and its evolution we find par excellence the creators of phylogenetic lines, for all prosoplasmas, as heretofore indicated, are the result of larval and not adult activity. Another generalization is the fact that prosoplasmas are practically confined to the Insecta; only a few low prosoplasmas of the Acarina are an exception.

Phylogenies of zoocecidia

Before presenting the outlines of the phylogeny in the various groups it will be desirable to point out some fundamental relationships between the kataplasmas and the prosoplasmas. KÜSTER,

although accurately distinguishing these two groups, curiously enough failed to see any relationship between them from an evolutionary standpoint. Nor has any other writer since this classification has been developed pointed out the very evident situation which exists. That the prosoplasmas in all cases are derived from the kataplasmas is self evident. This fundamental conception, together with an interpretation of it to be given later, forms the central thesis of this paper. On it has been built the diagrammatic presentation of the phylogenetic lines of the higher cecidozoon groups. Following the explanation of these which follows, a more detailed discussion of the general theoretical situation will be presented.

The phylogenetic lines

Attention should be called to the polyphyletic origin of galls, the cecidia-making habit having appeared independently in many diverse groups. Within certain phyla (ex. Nematoda) it appeared among a few closely related genera, while in certain families (ex. Itonididae) it probably had an independent origin in many genera. The "phylogenetic trees" of the various groups (pls. XXI, XXII) are arranged horizontally with some regard to the evolutionary position of the cecidozoon groups. Vertically, the figures are arranged on the basis of their classification into kataplasmas or prosoplasmas. The figures of the galls, while drawn more or less diagrammatically, are based on actual species. They have been chosen to represent fundamental types only. Practically all of them show the galls as seen in section, this being necessary to bring out such salient characters as position of cecidozoon, orientation with regard to plant parts, and the differentiation of sclerenchyma in certain prosoplasmas, this latter being indicated by a dark layer within the body of the gall. The lines or "trees" are based on cecidozoon groups of varying degrees of position in the systematic scale. None below families have been attempted, although an ideal study would present the genus as the unit. At the present time, however, this is not possible through lack of anatomical data. In the discussion of each group some mention will be made relative to the number of genera involved.

ROTIFERA (pl. XXI).—Only one rotifer gall is known. It consists of simple enlargements of the ends of filaments of *Vaucheria* (1) which harbor at their center the cecidozoon. They are to be regarded as extremely simple kataplasmas.

COPEPODA (pl. XXI).—Represented by one form only, a simple kataplasma (1).

NEMATODA (pl. XXI).—Represented by two genera, one using the roots (1), the other the aerial parts (2), producing simple kataplasmas in both instances. The root inhabiting form produces the greatest modification.

ACARINA (pl. XXI).—These galls are chiefly the work of the members of the genus *Eriophyes*. Two fundamental lines of evolution are evident: the production of numerous aborted parts (kataplasmas) from stems, buds, and leaves (1, 2); and a leaf gall line beginning with the erineum (mat of trichomes) stage (3) and passing into the diverticulum condition (5) or the leaf edge-roll state (6). From the leaf blade the erineum-forming type may change its point of attack to the rachis or petiole with more or less hyperplasia and hypertrophy of the hypodermal cells. Such an unusual form is seen in (4). The shallow diverticulum has given origin to the elementary prosoplasma leaf types as represented by (7–10). The figures with their connecting arrows are self-explanatory. It is believed that a type like that shown in (9), which is devoid of trichomes, has been derived from the trichome-bearing kinds. The prosoplasmas of the *Acarina* are of the simplest variety. In the entire absence of sclerenchyma layers and in the non-deviation from the primitive pouch type they constitute as a group the lowest of the prosoplasmas.

ORTHOPTERA (pl. XXI).—Only one genus is represented (1), forming an inconsiderable kataplasma consisting of aborted stem and leaves.

NEUROPTERA (pl. XXI).—A simple cortical swelling constituting a very primitive kataplasma (1) is only reported for this group.

THYSANOPTERA (pl. XXI).—These tropical galls are all of the kataplasmic type, the most primitive of which is the simple leaf fold (1), from which the more specialized condition shown in (2) has been derived. A simple curled edge probably represents

another derived type (3), although this may be interpreted as having an independent origin.

COLEOPTERA (pl. XXI).—Despite the vast size of this order and the intimate food relation many of its members hold with living plants, there has been but a slight development of the gall-making habit. They may all be included under the type shown (1), which is a simple cortical kataplasma.

LEPIDOPTERA (pl. XXI).—These are all stem galls of simple constitution. A number of the insect families are involved. The hyperplasia commonly affects all tissues about equally, so that there is merely a local enlargement of the stem (1), with a cavity occupying the pith region. The differentiation is uniformly weaker than in the normal stem; it is a low kataplasma.

The Lepidoptera and the Coleoptera are commonly given a higher position than the Hemiptera which follow. Since they show no complex gall phylogenies, they are placed out of position near a few other unimportant groups.

PSYLLIDAE (Hemiptera) (pl. XXI).—Three original lines of attack on the plant appear to have been made in this group, two of which (1 and 10) end blindly in inconsequential kataplasmas. The third primitive form, simple leaf fold (2), is probably ancestral to the simple leaf edge-roll (9) and a diverticulum kataplasma (3), from which type certain highly specialized prosoplasmas are believed to have sprung. The psyllid prosoplasmas, which are only known from America where they occur on the buds and leaves of the hackberry (*Celtis*), constitute in themselves an excellent evolutionary series, the main outlines of which are indicated in the diagram (4–8). The presence in all of them of specific sclerenchyma layers, together with other highly defined tissue form characters, makes them striking examples of prosoplasmas. No related kataplasmas, that is, on the same host, are now existent.

APHIDIDAE (Hemiptera) (pl. XXI).—All of the galls of this group probably have sprung from the simple leaf fold (1), which, since the insects are commonly numerous locally, appears in the highly variable compound form or the crumpled, wrinkled, or otherwise distorted blade. The number of these primitive aphid leaf convolutions is legion. From these have sprung the indefinite edge-

roll condition (7) and the variable pouch type (2). This latter in turn has given origin to such a kataplasma as shown in (3), which represents the work of many individuals, and the prosoplasma (5), which represents the work of but one insect, the stem mother. From the former has been derived such a spine-bearing prosoplasma as outlined in (4), from the latter the walled forms, the "umwallungen Gallen" of KÜSTER (6), have had their origin. In these no diverticulum structure whatever appears, but the larva is walled in by a vertical upgrowth from the blade. Once this type of gall is attained, the insect is able to use the more rigid parts of the plant, namely, petioles and stems of the season, as a basis for gall formation. None of the aphid prosoplasmas have reached the level at which a sclerenchyma layer is differentiated in them.

COCCIDAE (Hemiptera) (pl. XXI).—Three fundamental primitive kataplasmas can be distinguished in the Coccidae forms, the simple umbo on the stem (1), the shallow leaf pocket (5), and the saucer-shaped incept of the up-walled type. From the latter have arisen those remarkable Australian prosoplasmas characterized by differentiation on the sex basis, that is, the male and female larvae produce differently shaped and constructed galls (4*a*, male; 4*b*, female). One of these (3) shows the development of appendages borne on radiating arms. Its form is more primitive than the gall of (4), and in the absence of anatomical data pertaining to any of these forms, it is tentatively given a lower position. I can only find the statement that the female galls are "woody"; the information as to whether or not specific sclerenchyma layers are differentiated has not been obtained.

MUSIDAE (Diptera) (pl. XXII).—Gathered together under this superfamily name are a number of related dipterous families which are represented by kataplasmas only. Three fundamental beginning stages can be distinguished, related to the plant part attacked: a simple rosette resulting from the abortion of the stem axis with concomitant abortion of leaf elements (1), a simple cortical swelling (2), and the hyperplasia of the floral disk in certain Compositae (4). As an advance on the second are those cases in which the larva goes deeper, taking a central position in the stem, giving the intercalate globular type (3).

ITONIDIDAE (Diptera) (pl. XXII).—Numerically this is the largest group of gall producers. Many of the galls attain high evolutionary level, but not as high as many cecidia of the Cynipidae (Hymenoptera), which rivals this group in number and complexity. The most primitive gall of the Itonididae (Cecidomyiidae) is the simple leaf fold, a principal vein constituting the gall axis (1). Conceivably all others may be derived from this, if we grant the possibility of the necessary changes in the insect's instinctive behavior so that other plant parts are persistently attacked and used. Certain of these primitive galls, however, might have appeared independently. Both situations are shown in the diagram.

From the initial leaf fold was evolved the variable ill-defined pocket type (2), which in turn gave rise to the simple prosoplasma of (3). This advances either through the differentiation within it of a sclerenchyma layer (4), or through the partial transfer of the gall toward the upper side of the leaf (5). From this type we have a striking advance through the sclerenchymatized cecidium (6) to the type characterized by a dehiscing larval cell formed by the lignified tissue together with the lining of parenchymatous nutritive tissue. In (8) we have the attainment of the full up-walled ("umwallungen") condition which is believed to have been derived, as indicated, from the diverticulum or pouch form. The majority of up-walled galls show the advanced state, however, through their containing a scleride zone (9). From the up-walled type (8) there has also been derived the interesting double chambered form (11), with the type shown in (10) as an intermediate condition. Excellent examples illustrating all stages of this latter evolution series have been described by the writer (11) from the hickory (*Carya*).

Originating either independently or from the itonid insect which produces the simplest leaf type, we have the burrowing form which causes the "blister" gall (14). A form of this kind attacking the embryonic fruit gives the situation shown in (15), or becoming more specialized on the leaf gives us the prosoplasma (16), or attacking the stem initiates a series of stem galls (17–20), going over into the prosoplasma region with the attainment of

sclerenchyma layers around the larval chambers. If the apical meristem is used as a basis of operation, we get such a primitive gall as shown in (21), and, either through a burying process on the part of the larva or through the up-walling mode of overgrowth, we pass through such a stage as (22) to the prosoplasmatic condition of (23), ending in such a highly specialized type as shown in (24).

CHALCIDAE (Hymenoptera) (pl. XXII).—This family is represented very insignificantly by a few genera producing simple cortical enlargements (1).

TENTHREDINIDAE (Hymenoptera) (pl. XXII).—A few genera of gall makers represent this family. Some species form simple, cortical stem hyperplasias (1); others a rather well defined leaf gall with such homogeneous tissue within it that it may be regarded as but a high kataplasma (2). One European form produces a very low kataplasma in inducing an enrolled condition of the leaf (3). The second form is of especial interest because its initial stages are known to be induced through the action of a chemical stimulus emitted by the adult female at the time of egg-laying.

CYNIPIDAE (Hymenoptera) (pl. XXII).—This family is recognized by all students to be the most remarkable from the standpoint of variety and complexity of the galls produced. This is true even though the largest number of these galls is found on one host genus (*Quercus*). The vast majority of cynipid galls are prosoplasmas. Four independent points of origin are presented, though three of these may conceivably have been derived from the primitive leaf kataplasma (10), as indicated by the arrow lines.

In the evolution of the stem galls we find a progressive series (1–4) related to the orientation of the larva within the stem. This situation is related primarily to the placing of the egg by the ovipositor of the adult females, for so far as known these larvae are not migratory. Any of the stem kataplasmas shown may become elementary prosoplasmas through the differentiation of a sclerenchyma layer around the larval chambers, a parenchymatous nutritive layer being left as a lining. In the diagram only the medullary (4) and cortical (5) types of prosoplasmas are shown. From the latter has been evolved the interesting dehiscence form shown in (6).

The bud and apical meristem galls are shown in (7–9). In (7) a number of the bud leaves merely become fused, while the other two show the transition from the sclerenchymatized polythalamous condition with relatively long, aborted leaves forming an involucre to the sclerenchymatized monothalamous state with shorter, involucre-like elements. In many prosoplasmas of this type the involucral structures are suppressed altogether.

The most primitive cynipid gall is believed to be the variable, generally polythalamous, slightly differentiated kataplasma shown in (10). From this type through the attainment of the "protective" layers the simple prosoplasma (13) is reached, from which by reduction to the monothalamous stage an important stock type (14) is obtained. This latter, however, may also have been evolved through reduction of chamber number before sclerenchymatization had taken place (11). The gall is shown in its primitive intercalate position in the leaf. The prosoplasma variant from the latter is shown in (12).

From the concentrically built stock type (14), which is regarded as an appendicular form, the greatest evolution in prosoplasmas has taken place. Six fundamental lines appear to have sprung from it. Certain characters evolved in and characteristic of these different lines are in special instances combined in the same gall. For example, the stalked type (19) may also exhibit the free larval cell condition of (22), as found in *Dryophanta pedunculata* Bass. The combination, however, of two or more of these fundamental type characters in the same gall is the less common condition; for the most part the galls can be associated with one or the other of the structural evolutionary lines. The same tendency, previously observed in the Itonididae, toward the formation of a distal false chamber, is found (15). This culminates in such a bizarre bracteate form as that shown in (16), a new gall discovered recently by the writer in North Carolina.

Another striking series is that of the evolution of the radiate-fiber type of gall. This begins with the appearance of aeriferous tissue in the cortical region (17), and ends with the condition in which only the fibrovascular bundles traverse the cortical region (18). The type shown in (22) may have been derived from the

latter through the elimination of the bundles, but it may also have had an independent origin from the stock type; embryological evidence in this connection is not available.

The pedicellate condition (19) constitutes the culmination of another line, in which all possible stages may be found in the oak cynipids.

A special place has been given to those galls (20) which bear appendages on the gall body proper (larva containing region). It is believed these bracteate forms for the most part are derived from the non-bracteate forms. There are, however, such possible exceptions as the gall of *Rhodites rosae* L. or *R. bicolor* Harr., in which instances the appendages might be interpreted to be but the reappearance of certain normal parts. In so far as this is true they would be kataplasmic.

In (21) is represented a type possessing highly elongated trichomes. All gradations from the smooth stock type (14) to extreme pubescence are known in the cynipid cecidial biota.

It is better for the present to consider the free larval cell type (22) as an independent line, although, as already indicated, it may have been derived from the radiate-fiber form.

A final line is that leading to the obliteration of the parenchymatous cortical region (23), resulting in a firm, thin-walled structure. These galls are all very small.

Before closing the account of the Cynipidae, mention should be made of the kataplasma shown in (24). Larva cells are organized in the homogeneous tissue of the acorn. This may have arisen independently, or with greater probability it was derived through a change in point of attack on the part of insects forming a primitive leaf gall.

Summary of phylogenetic data

It will be desirable to point out certain major evolutionary tendencies appearing in widely separated groups which point toward an orthogenetic interpretation. (1) The tendency toward specific sclerenchymatization in the formation of the lignified tissue forming the so-called protective layers in the galls. This has appeared independently in Psyllidae, Itonididae, and Cynipidae,

in all of which it is a prominent character in the majority of their prosoplasmas. (2) The tendency toward the up-walled ("umwallungen") condition. This is partially attained in the Acarina and Psyllidae, fully attained in the Aphididae, Coccidae, Itonididae, and is superimposed as the distal false chamber on certain galls of the Itonididae and Cynipidae. (3) The tendency toward the dehiscent type. This is much more restricted, appearing only in the Itonididae and the Cynipidae. (4) The tendency toward appendicular structures borne by the galls. This tendency is almost confined to the Cynipidae. It has appeared in a weak degree in other groups, as in the Aphididae and in certain hickory itonids in which the gall base flares out into ill-defined processes. In the Cynipidae a great variety of appendages is found for which it is not possible to find homologues anywhere on the host plant. Many minor tendencies can be traced out in gall phylogeny studies which may only be mentioned in this general paper. Among such are those toward certain forms, those toward certain orientations of tissues, those toward specializations with regard to certain chemical content (high tannin deposition, etc.), and those associated with the transition from the polythalamous to the monothalamous condition.

Recapitulation data

If zoocecidia are amenable to the same evolutionary interpretations as are used in the study of plant and animal parts, then VON BAER'S law should apply to the situation, and this is exactly what is found. Striking examples of recapitulation phenomena may be found in all the larger gall groups, yet, strangely enough, so far as the writer knows, no one has called attention to them or even to the possibility of the law applying in the zoocecidial field. The most fundamental fact in this connection is that all prosoplasmas in their ontogeny recapitulate the kataplasma stage. The initial stages of all prosoplasma galls (so far as known), which begin on partially differentiated host tissue, involve a process of dedifferentiation; the tissue is thrown back into a homogeneous condition (full kataplasmic state) out of which grows the new structure. Of course in those instances in which the larva

is from the beginning in contact with meristem, no such regression is possible or necessary. This situation will be developed at greater length in the general discussion.

Within the prosoplasmas themselves innumerable examples of recapitulation may be pointed out, two of which may be mentioned. In the ontogeny of the cecidium *Amphibolips inanis*, the gall passes through the spongy stage illustrated by *Amphibolips confluentus* before it reaches the mature condition with radiating fibers. In the ontogeny of *Oligotrophus annulipes* (European) a juvenile stage is passed through which is almost exactly reproduced in an adult gall (*Cecidomyia* sp.) on the same host. HOUARD (7), in reporting the resemblance of these two stages, fails to suggest the evident recapitulation interpretation.

Discussion

The foregoing part of this paper presents the results gained in the application of certain fundamental conceptions regarding cecidia which are concerned with the evolution of these structures. These conceptions have their historical background, as already indicated, but it will be well to review them in the light of modern genetic and phylogenetic theories, and point out their synthesis which, with the application of them in constructing the phylogenetic trees, constitutes the chief contribution of the present paper.

Before entering upon this constructive work, however, it will be necessary to clear the ground of certain false conceptions which have held sway to the present time, such as the interpretation of KÜSTER, COSENS, and others, who hold that all gall characters are but the expression of active or latent normal host plant characters. COSENS and SINCLAIR (4) state that there remains no authentic instance of any organ or tissue in a gall that is new, ontogenetically or phylogenetically. This interpretation is clearly fallacious, for it is the essential newness of prosoplasmas which constitutes their most important characteristic. This newness appears perhaps in its most striking manner in the form characters of the tissues, which implies of course the form of the gall as a whole. Since form characters are of utmost importance

throughout all taxonomic, genetic, and evolutionary studies, certainly these characters must be taken into account by the cecidologist. When the counterparts of these characters cannot be found associated with any normal tissue mass of any plant, they must be regarded as new and not as having had their origin from the plant side. As pointed out by the writer in a previous paper (12), "in prosoplasmas the types of cells found are closely comparable to those of normal plant parts, but the tissue forms (in prosoplasmas) are fundamentally new." KÜSTER (10) speaks very properly of "Die prosoplasmatische Neubildungen," recognizing the fundamentally independent character of the higher galls, but like COSENS fails to recognize that the origin in evolution of the prosoplasmas lies elsewhere than in the constitution of the plant or of the plant's ancestors.

COOK (2) arrived at a proper basis for advance when he saw that "the morphological character of the gall depends upon the genus of insect producing it, rather than upon the plant on which it is produced." COOK, however, failed to use BEYERINCK'S (1) early division of galls into the "indefinite" and "definite" groups (a fundamental situation which KÜSTER later developed), so that his work fell short of a full analysis; for, as has been indicated, the phylogenetic origin of the prosoplasmas from the kataplasmas (within cecidozoon groups) is all important.

This leads to the nucleus of the present interpretation, which holds that in the contemplation of zoocecidia two fundamental groups must be recognized, kataplasmas and prosoplasmas, and that there exists a phylogenetic relation between them. The most interesting and significant situation in this connection is that, whether viewed ontogenetically or phylogenetically, kataplasmic development progresses, through a process of increasing inhibition of host characters, from the normal host differentiation to complete homogeneity, upon the attainment of which prosoplasmic development may commence the construction of new differentiations and new forms. The embryological and comparative morphological evidence for this interpretation is overhwelming, as has been indicated in the foregoing accounts of phylogenies and of recapitulation phenomena.

It would appear then, in zoocecidial ontogeny or zoocecidial evolution, that there occurs at first an overcoming or breaking down of the differentiation and morphogenetic mechanisms which bring about the normal expression of the host plant characters. When this has gone on to the point where no differentiation whatever ensues, the new advance is made in the direction of the prosoplasmas in which fundamentally new characters are caused to appear. Thus we have a remarkable turning point in gall evolution, namely, that at which the normal expression of the plant's potentialities, locked up in its meristem, is inhibited. All gall forms, from the most insignificant interference with normal differentiation to total suppression, are kataplasmas, and all those types arising as definite new structures from the final kataplasmic condition are prosoplasmas.

As pointed out in connection with the recapitulation data, all prosoplasmas in their ontogeny pass through the kataplasmic stage, either in the actual reversion of partially differentiated tissue to the undifferentiated condition; or, if the cecidozoon is in contact with the meristem, there occurs the equivalent, namely, the complete suppression of the plant's tissue characters, only the new ones of the prosoplasma appearing.

For the sake of clarity the situation has been presented in positive, mutually exclusive terms. There exists, as would be expected, a small minority of galls which occupy the transition region between the kataplasmas and the prosoplasmas. In certain of these, for example, prosoplasmic characters may exist along with kataplasmic ones. Such a gall is that of *Phytophaga rigidae* O.S. discussed by COSENS and SINCLAIR (4), in which aeriferous tissue is found which they explain on the latent character hypothesis. According to this view the gall is kataplasmic, but if we take into consideration the specialized structure, the "beak," of the distal end of the gall (an "umwallungen" development), the form character of the scleridal and nutritive tissues (counterparts of which are not to be found in any normal part of the host or its relatives), we must conclude that this gall is also definitely prosoplasmic in nature. Thus in many forms both types of tissue characters may appear. It will be questioned at

once in the evolution or ontogeny of zoocecidia, how is such a retrogression followed by a progression in a new direction possible? What is the mechanism involved? The effort of all students in attacking this so-called stimulus problem has signally failed to elucidate the situation. In the opinion of the writer this is because the problem goes much deeper than our present technique is able to penetrate, for it is to be classed with the general unsolved problems of growth (ontogeny) and evolution (phylogeny). Just as a mass of cells in an apical growing point, in some unknown manner, certainly has much to do with the differentiation products of that stem, so has the mass of embryonic cells constituting the prosoplasma-making larva much to do with the differentiation products, not only of itself but of the plant tissue around it. It has extended its control (mechanistically interpreted) in the field of form characters (and others to a less degree) beyond the borders of its own body. As FOCKEU (**6**) has put it: "La feuille est en rapport avec les phenomenes vitaux de la larve" rather than with the normal leaf itself (we would append to bring out the contrast). In other words, we would hold that the development of prosoplasmas is brought about through the superposition of embryonic animal tissue (the cecidozoon larva) on that of embryonic plant tissue with a relation in growth which is an essentially normal one, that is, the mechanism of morphogenesis is operative, but the primary control is with the larva.

This leads to a final statement, one given earlier by the writer (**12**), to the effect that "the germ plasm of the cecidozoon is the place of origin of gall forms." This, of course, merely falls in with the current general ideas concerning the significance of the germ plasm in evolution. In the germ plasm of the animal originated the factorial conditions which, phylogenetically considered, first gave the embryonic cecidozoon the ability to break up the normal operation of the plant's factors making possible normal plant differentiation, and secondly the factors which initiate the development of new form and other characters expressed in the plant cell masses.

Zoocecidial evolution then is a complex in which, in its early stages (kataplasmas) with regard to certain characters, the plant's

germ plasm dominates, while in its later stages (prosoplasmas) the animal's germ plasm gains control; the whole, however, constituting a single progressive series of factorial transformation as far as the changes in the animal germ plasm are concerned.

Summary

1. KÜSTER's groups, kataplasmas (lower galls of indefinite nature, differentiation conditions similar to, but in complexity below that of normal plant) and prosoplasmas (higher galls of definite nature, differentiation conditions new) are basic for the present paper.

2. Evolutionary concepts are introduced in pointing out that prosoplasmas have arisen from kataplasmas. The probable main outlines (phylogenetic trees) of the natural cecidozoon gall groups are presented for the first time.

3. Kataplasmic evolution is held to be a process of progressive inhibition of differentiation ending with tissue homogeneity. Prosoplasmic evolution may only begin when homogeneity has been attained, and consists in the development of new form and tissue orientation characters chiefly. In prosoplasma formation, whether viewed ontogenetically or phylogenetically, the insect larva has gained control of the differentiation and morphogenetic mechanisms, so that animal factors come to expression in plant tissue.

4. Origin of significant characters of prosoplasmas lies in change in factorial situation in animal's germ plasm.

NORTH CAROLINA STATE COLLEGE
RALEIGH, N.C.

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EXPLANATION OF PLATES XXI, XXII

Plate XXI

Rotifera: (1) *Notammata Werneckii* Ehrenb. on *Vaucheria*.

Copepoda: (1) *Harpacticus chelifer* Müller on *Rhodomenia*.

Nematoda: (1) *Heterodera radicicola* Greef on *Lycopersicum;* (2) *Tylenchus devastatrix* Kühn on *Trifolium*.

Acarina: (1) *Eriophyes* sp. on *Fraxinus;* (2) Eriophyes *populi* Nal. on *Populus;* (3) *Eriophyes* sp. on *Fagus;* (4) *Eriophyes* sp. (*anomalum* Cook) on *Juglans;* (5) *Eriophyes* sp. (*querci* Garman) on *Quercus;* (6) *Eriophyes goniothorax* Nal. on *Crataegus;* (7) *Eriophyes* sp. on *Cephalanthus;* (8) *Eriophyes* sp. (*abnormis* Garman) on *Tilia;* (9) *Eriophyes* sp. on *Salix;* (10) *Eriophyes* sp. on *Acer*.

Orthoptera: (1) *Meconema varium* Fabr. on *Quercus*.

Neuroptera: (1) *Lestes viridis* Van der Lind on *Fagus*.

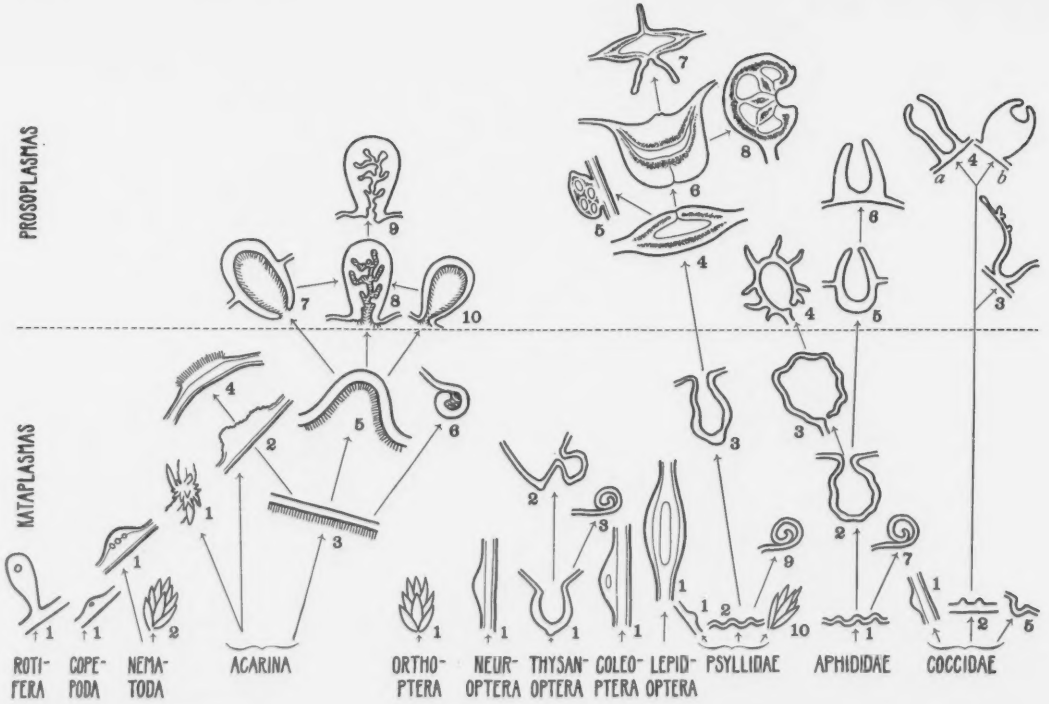
Thysanoptera: (1) *Thrips* sp. on *Piper;* (2) *Thrips* sp. (host not given); (3) *Mesothrips melastomae* Zimm. on *Melastoma*.

Coleoptera: (1) *Mecas inornata* Say on *Populus*.

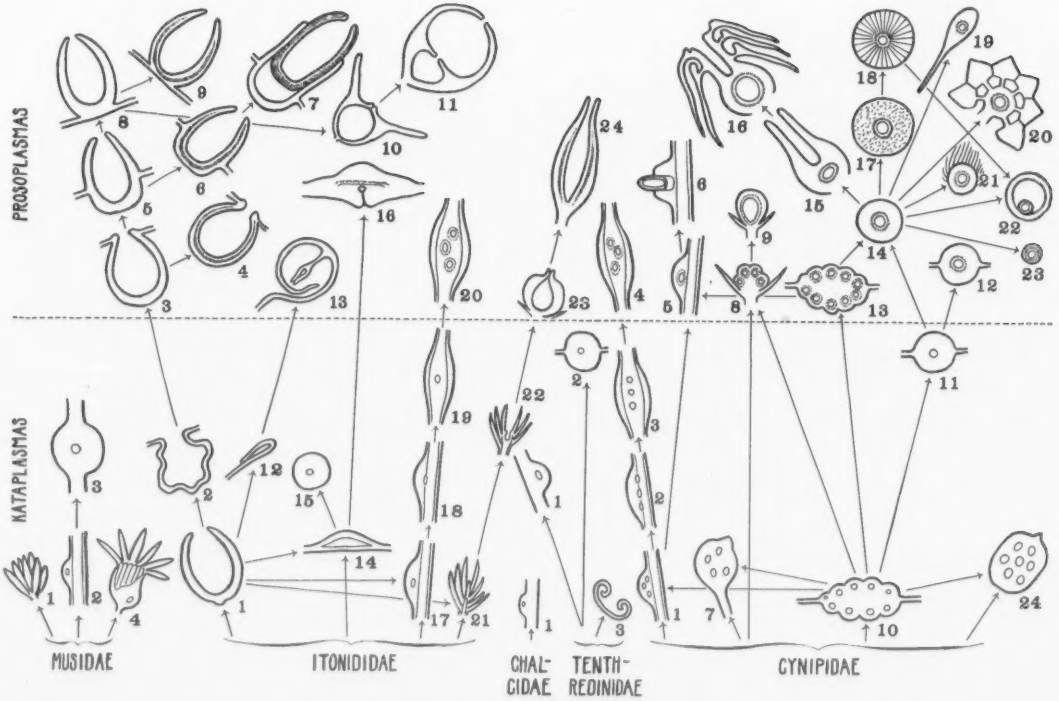
Lepidoptera: (1) *Gnorimoschema gallaesolidaginis* Riley on *Solidago*.

Psyllidae: (1) *Psylla crataegi* Schrank on *Crataegus;* (2) *Psylla ledi* Flor. on *Ledum;* (3) *Trioza Kiefferi* Giard on *Rhamnus;* (4) *Pachypsylla vesiculum* Riley on *Celtis;* (5) *Pachypsylla gemma* Riley on *Celtis;* (6) *Pachypsylla mamma* Riley on *Celtis;* (7) *Pachypsylla asteriscus* Riley on *Celtis;* (8) *Pachypsylla venusta* Riley on *Celtis;* (9) *Trichopsylla Walkeri* Forster on *Rhamnus;* (10) *Livia maculipennis* Fitch on *Juncus*.

Aphididae: (1) *Myzus ribis* L. on *Ribes;* (2) *Pachypappa marsupialis* Koch on *Populus;* (3) *Pemphigus vagabundus* Walsh on *Populus;* (4) *Hamamelistes spinosus* Shimer on *Hamamelis;* (5) *Phylloxera conica* Shimer on *Carya;* (6) *Phylloxera caryaecaulis* Fitch on *Carya;* (7) *Chaitophorus leucomelas* Koch on *Populus*.



WELLS on ZOOCECIDIA



WELLS on ZOOCECIDIA

Coccidae: (1) *Planchonia fimbriata* on *Coronilla;* (2) *Asterodiaspis quercicola* Bonché on *Quercus;* (3) *Apiomorpha cornifex* on *Eucalyptus;* (4) *Brachyscelis oricola* on *Eucalyptus* (*a*, gall produced by male; *b*, gall produced by female).

Plate XXII

Musidae: (1) *Lipara lucens* Meigen on *Phragmites;* (2) *Agromyza Kiefferi* Tavares on *Cytisus;* (3) *Eurosta solidaginis* Fitch on *Solidago;* (4) *Phorbia seneciella* Meade on *Senecio.*

Itonididae: (1) *Dasyneura gleditschiae* O.S. on *Gelditsia;* (2) *Contarinia negundifolia* Felt on *Negundo;* (3) *Lobopteromyia venae* Felt on *Crataegus;* (4) *Mikiola fagi* Hartig on *Fagus;* (5) *Cecidomyia* sp. on *Amelanchier;* (6) *Cecidomyia* sp. on *Populus;* (7) *Cecidomyia* sp. on *Celtis;* (8) *Rhopalomyia anthophila* O.S. on *Solidago;* (9) *Cecidomyia unguicola* Beutm. on *Celtis;* (10) *Cecidomyia* sp. on *Carya;* (11) *Caryomyia inanis* Felt on *Carya;* (12) *Itonida foliora* Russell and Hooker on *Quercus;* (13) *Cecidomyia* sp. on *Populus;* (14) *Cincticornia* sp. on *Quercus;* (15) *Contarinia virginiana* Felt on *Prunus;* (16) *Cecidomyia verrucicola* O.S. on *Tilia;* (17) *Neolasioptera cornicola* Beutm. on *Cornus;* (18) hypothetical; (19) *Lasioptera clavula* Beutm. on *Cornus;* (20) *Rhabdophaga batatas* Walsh on *Salix;* (21) *Rhabdophaga strobiloides* Walsh on *Salix;* (22) *Rhopalomyia* sp. on *Solidago;* (23) *Rhopalomyia hirtipes* O.S. on *Solidago;* (24) *Phytophaga rigida* O.S. on *Salix.*

Chalcidae: (1) *Isosoma tritici* Fitch on *Triticum.*

Tenthredinidae: (1) *Cryptocampus nodus* Walsh on *Salix;* (2) *Pontania pomum* Walsh on *Salix;* (3) *Blenocampa pusilla* Klug on *Rosa.*

Cynipidae: (1) *Neuroterus batatas** Fitch on *Quercus;* (2) *Andricus punctatus* Bass. on *Quercus;* (3) *Aulacidea tumida* Bass. on *Lactuca;* (4) *Neuroterus majalis* Bass. on *Quercus;* (5) *Neuroterus rileyi* Bass. on *Quercus;* (6) *Andricus excavatus* Ashm. on *Quercus;* (7) *Andricus clavula* Bass. on *Quercus;* (8) *Andricus frondosa* Bass. on *Quercus;* (9) *Andricus topiarius* Ashm. on *Quercus;* (10) *Aylax taraxici* Ashm. on *Taraxacum* or *Callirhytis tumifica* O.S. on *Quercus;* (11) *Callirhytis tumifica* O.S., monothalamous form on *Quercus;* (12) *Rhodites rosaefoliae* Cockll. on *Rosa;* (13) *Neuroterus irregularis* O.S. on *Quercus;* (14) *Biorhiza mellea* Ashm. on *Quercus;* (15) *Xystoteras volutellae* Ashm. on *Quercus;* (16) *Cynips* sp. on *Quercus;* (17) *Amphibolips confluentus* Harris on *Quercus;* (18) *Amphibolips inanis* O.S. on *Quercus;* (19) *Andricus capsulus* Bass. on *Quercus;* (20) *Cynips Hartigi* Hartig on *Quercus;* (21) *Neuroterus floccosus* Bass. on *Quercus;* (22) *Dryophanta palustris* O.S. on *Quercus;* (23) *Neuroterus saltatorius* Edwards on *Quercus;* (24) *Callirhytis fruticola* Ashm. on *Quercus.*

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THE GAMETOPHYTES OF EQUISETUM LAEVIGATUM[1]

ELDA R. WALKER

(WITH PLATES XXIII, XXIV AND THREE FIGURES)

Introduction

According to BUCHTIEN (1), gametophytes of *Equisetum* were first found by VAUCHER in 1826, and later by BISCHOFF in 1829, and MILDE in 1852. The finding of *Equisetum* gametophytes, however, has been rare. When in August 1916, ROBERT A. NESBIT, at that time a student in the University of Nebraska, found large numbers of them near Tekamah, Nebraska, it was hardly expected that the discovery would soon be repeated. The gametophytes, however, have since been found in several localities, usually in Nebraska, by a number of persons. At the suggestion of Dr. CHARLES J. CHAMBERLAIN the writer undertook a study of these gametophytes with the results here reported.

Distribution

The discovery of *Equisetum* gametophytes by Mr. NESBIT called the attention of local bôtanists to the possibility of finding them. The result is that they have been observed in recent years as follows:

Robert A. Nesbit, Tekamah, Nebraska, August and September 1916; *N. F. Petersen*, Osborn, Indiana, August 2, 1917; Manhattan, Kansas, September 1917; Reno, Nevada, July 1918; Pilger, Nebraska, September 25, 1920; Lincoln, Nebraska, October 9, 1920; Florence, Nebraska, November 5, 1920; South Sioux City, Nebraska, November 7, 1920; *F. C. Jean*, Peru, Nebraska, August 1917; *Elda R. Walker*, *Doris Hayes*, and *Katherine Wolfe*, Lincoln, Nebraska, October 12, 17, 24, and November 14, 1920.

Since learning of these recent observations, Professor O. A. STEVENS has told the writer of finding a considerable number of *Equisetum* gametophytes on the banks of the Big Blue River and a drainage ditch emptying into it, at Manhattan, Kansas, in Septem-

[1] Contributions from department of botany, University of Nebraska, new series, no. 33.

ber 1908. Mrs. T. J. FITZPATRICK also found large numbers of them on the banks of the Iowa River at Iowa City, Iowa, during the years 1884–1888. At Osborn, Indiana, Manhattan, Kansas, and Reno, Nevada, Professor N. F. PETERSEN found only a few specimens. At all other points, except Lincoln, they were present in large quantities. They were on the banks of every creek but one examined in the neighborhood of Lincoln, but were not abundant in any place. Mr. NESBIT describes the habitat in which they grew at Tekamah, Nebraska, as follows:

> These were found along both banks of a typical prairie creek from the point where it emerges from the hills for a distance of at least four miles upstream. They occurred almost continuously throughout this distance. The creek is subject to overflow several times a year, and has built up a narrow floodplain of rich soil. The creek bed itself is about 15 ft. below the level of the floodplain, and is shaded by trees throughout most of its course. Near the water there is usually a belt of mud or very moist soil, varying in width from a few inches to several feet, and sloping gradually upward to the beginning of the more precipitous slope of the banks. . . . . The gametophytes, varying in size from 1 mm. to about 1 cm. in diameter, occurred on this mud. They were abundant, in many places being separated by an average distance of not more than 3 cm. In other places they were more scattered, and occasionally, where the mud belt was too soft, they were lacking entirely. . . . . There were very few other plants growing in this mud belt, *Riccia* being the only form that appeared constantly.

For all the localities in Nebraska, Kansas, and Iowa the same description in general holds true. They were found along streams of all sizes, from the smallest creeks and drainage ditches to the Missouri River, and in all cases were on the mud belt and associated with *Riccia*. At Osborn, Indiana, the gametophytes grew in a ditch by a railroad on soil where ties had been burned. This had destroyed other vegetation, and mosses were just starting with the *Equisetum*. At Reno, Nevada, they were growing beside a waterfall.

Identification of species

In no case in Nebraska were mature *Equisetum* sporophytes found on the creek banks on which the gametophytes were growing. As a rule the only spore-producing plants within many miles were *E. arvense* and *E. laevigatum*, strictly prairie forms. Spores of *E. arvense*, *E. robustum*, and *E. laevigatum* have been grown in

culture, and the wild gametophytes were compared with them. They resembled closely the two latter, but were definitely different from *E. arvense*.

In eastern Nebraska but two other species of *Equisetum* are known, *E. robustum* and *E. variegatum*, according to FITZPATRICK (4). Of these *E. variegatum* is rare; *E. robustum* is seldom found except along the banks of the Missouri River and its larger tributaries. The gametophytes found on the river banks at Florence and South Sioux City were slightly larger than the others and might belong to this species. FITZPATRICK, however, who examined the young sporophytes of all of the collections, failed to find on these evidence of the characters of *E. robustum*. Like those of all the other Nebraska gametophytes, he found that they resembled more closely *E. laevigatum*. These last bore so many large sporophytes that the gametophyte tissue was badly disorganized and of little use for study; consequently the microscopic studies were limited to the gametophytes from Tekamah, Pilger, and Lincoln. As at these places *E. robustum* is not present, and as the gametophytes do not resemble *E. arvense*, they are undoubtedly *E. laevigatum*.

The gametophytes from Osborn, Indiana, are without question *E. arvense*. Adult plants of the species occurred near by, and the gametophytes agree with those grown in culture. Those from Manhattan, Kansas, Iowa City, Iowa, and Reno, Nevada, were not seen by the writer, nor were those from Peru, Nebraska. Abundant specimens from the other localities, however, have been examined.[2]

Gametophytes

The gametophytes appear as circular cushions (figs. 1–5, 7, 10, and text fig. 1) varying in diameter from 1 mm. to 1 cm. They are a dull green with a slight brownish tint, making them inconspicuous as they grow on the wet soil. In many cases the writer looked at a given spot several seconds before her eye differentiated the form of the gametophytes, even where there were some of the larger ones. This may account in part for their not having been found more frequently.

[2] Sections made by STEVENS of the gametophytes found by him at Manhattan, Kansas, have been examined. These agree entirely with the gametophytes of *E. laevigatum*.

Each gametophyte consists of a flat circular disk (shown entire in fig. 6, which is a ventral view, and in section in figs. 8 and 9) of large-celled compact tissue 1–10 mm. in diameter and bearing many upright green branches on its upper surface. It is usually indented deeply at one side (figs. 1, 5, 6) and may be more or less lobed at the periphery, where it is surrounded by a heavy band of meristem (figs. 6, 8, 9) so long as growth continues. This meristem is often more active at some points than at others, which causes the marginal lobing. Fig. 6 shows the under side of the gametophyte whose upper surface is shown in fig. 1. The thallus was killed and

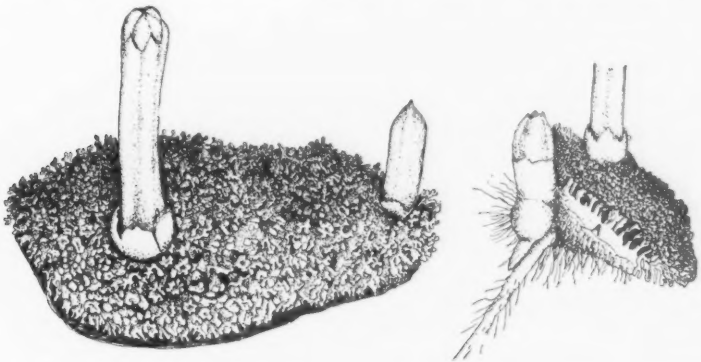

FIG. 1.—*E. laevigatum:* at left gametophyte with two sporophytes; at right gametophyte with sporophyte having developed a second shoot and root; gametophyte tissues cut away at *A*; section of sporophyte shown in fig. 11; ×10.

cleared in glycerine and then photographed from below to show the meristem band about the periphery and the slight lobing often present. It is this peripheral meristem that continues the growth of the thallus and gives rise to the upright branches and the sex organs. Fig. 8 shows this meristem at each end of the section producing archegonia. Fig. 9 shows the same structure, but at the left the meristem band contains two antheridia, and at the right a sporophyte with foot, root, stem, and leaves differentiated. The entire upper surface of the thallus is covered by the upright green branches. These branch more or less above and are wider at the tip than at the base (fig. 8). Very little chlorophyll is present in the

large cells composing the disk. The under surface is richly supplied with rhizoids.

The gametophytes are typically monoecious. Over fifty specimens of all sizes have been examined in paraffin sections and a large number of others in freehand sections, and still others without sectioning. None has been found without old archegonia. Many, about 30 per cent, also bear antheridia that are still active, and others show the scars of antheridia that have discharged their sperms. Only in a few cases was it impossible to find some trace of

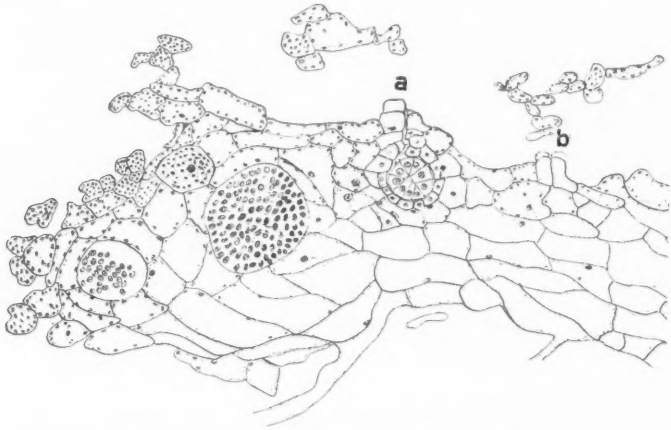

FIG. 2.—*E. laevigatum* (vertical section): at left two mature antheridia; at *a* archegonium containing young sporophyte; at *b* neck cells of functionless archegonium; ×75.

them. Antheridia, archegonia, and sporophytes often show in the same section. Fig. 9 shows antheridia on the left and a sporophyte on the right. The same thallus showed in other sections young and old archegonia. Fig. 17, whose detail is shown in text fig. 2, shows a vertical section through the periphery of a thallus. At the left are two mature antheridia. At the center above at *a* is an archegonium containing in its venter a young sporophyte of about thirty-two cells. At *b* are the four neck cells of an old functionless archegonium. Text fig. 3 shows part of a section of another thallus. On the left is a young antheridium in which the sperm

mother-cells are not yet differentiated. Two cells to the right of it is the venter of an archegonium surrounded by its jacket cells and containing a mature egg cell. Above at *a* are the neck cells in oblique section.

Figs. 12 and 13 are near sections, cut horizontally. In fig. 12 are shown twelve antheridia in various stages of development.

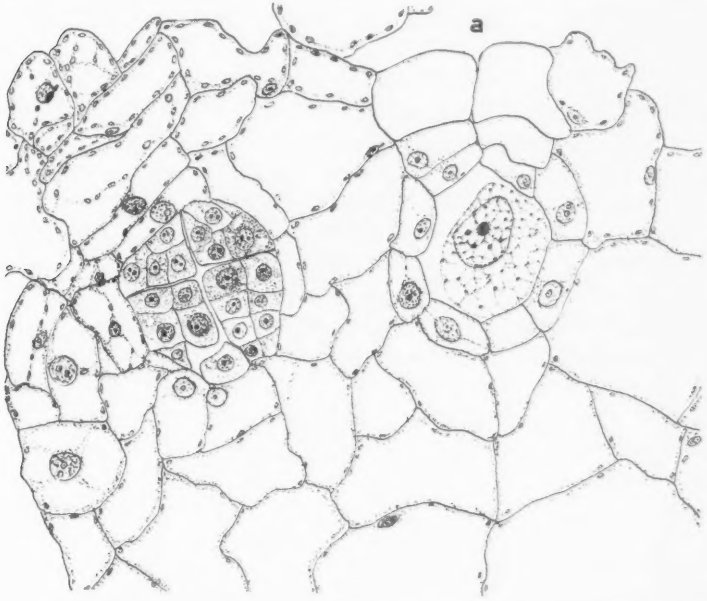

FIG. 3.—*E. laevigatum* (vertical section): at left young antheridium; at right archegonium with egg; below *a* neck cells cut obliquely; ×380.

In the smaller lobe only two cells from a young antheridium is the neck (*a*) of an archegonium, whose venter containing a mature egg is shown in a deeper section, fig. 13 below *a*. Fig. 14 shows a vertical section of an archegonium containing a young sporophyte. Fig. 15 is a vertical section showing two mature antheridia at the left. Directly below *a* and *a* are the necks of two old archegonia that have failed to be fertilized. In fig. 16 above is a mature antheridium and a very young one. At the extreme left (*B*) and

also to the right (*B*) of the lobe bearing the antheridia are old antheridia whose outer walls have broken away. Some sperm cells are still present. At the extreme right below *a* is one of the four neck cells of an old archegonium whose venter has become brown with age. This same method of antheridial dehiscence is shown in fig. 19*B*.

On the peripheral meristem young archegonia or antheridia or both (figs. 8, 9, 12–19, text figs. 2, 3) develop so long as the meristem continues its growth, but are not distributed in any definite way. In some individuals only one kind of sex organ will appear throughout the entire periphery, while on others certain lobes develop archegonia and others antheridia. On still other gametophytes archegonia and antheridia occur together (text figs. 2, 3 and figs. 12, 13, 15, 17), mixed indiscriminately around the entire meristem ring on the various thallus lobes. One gametophyte, for example, bore eleven sporophytes in various stages of development, fifteen active antheridia, and numerous archegonia in all stages, from old functionless ones to those still in stages of development. In the gametophytes from Tekamah, Nebraska, of the 30 per cent bearing young active antheridia 70 per cent also bore sporophytes. Those from other localities showed approximately the same condition.

Old ruptured antheridia and old archegonia show within a few cells of young active sex organs (figs. 15, 16, 17). When the antheridia mature and discharge their sperms, the outer wall breaks away, leaving but a slight scar in the tissue. The other tissues may or may not push up over this. In the former case the walls of the antheridium collapse and show as a brown line between the vegetative cells; in the latter case the scar is only a ragged break in the periphery (figs. 16, 19). These are recognized with difficulty, which no doubt accounts for the apparent absence of old antheridia on some of the thalli. On many bearing only archegonia, however, it was possible to indentify definitely the scars of old antheridia. There were a few actively growing individuals on which antheridia were not definitely located. In the case of gametophytes bearing large or numerous sporophytes, the tissue was so shrunken and broken down that it was often difficult to identify old arche-

gonia, which are usually conspicuous, and in such cases no traces of antheridia could be found.

In general it seems that the thallus continues to grow, forming new sex organs until sporophytes have developed to such an extent that the tissues are exhausted. If a sporophyte starts when the thallus is small, one rarely finds young sex organs developing later. If, however, fertilization does not occur, the archegonia dry up and new ones, and often antheridia also, are formed until fertilization is accomplished. If the thallus has attained considerable size before any fertilization occurs, a large number of sporophytes may be supported by it without injury, and in such cases the development of sex organs may continue until many archegonia have been formed and fertilized, and until the sporophytes are well advanced. The sporophytes invariably occur near the periphery, as shown in figs. 4, 7, 9, 10, and 11 of the thallus, while old functionless archegonia often show between the branches entirely across the surface.

The younger sporophytes are nearer the edge of the disk, and the active archegonia and antheridia are in the peripheral meristem (figs. 8, 9, 12–19, and text figs. 2, 3). Eleven sporophytes in early stages have been seen on one gametophyte, but not more than seven have been found sufficiently large to be seen by the unaided eye. In a few cases dead young sporophytes were observed, but in the majority of cases they looked in good condition. As the growing season was nearing its close, however, it is hardly probable that sporophytes not yet having secured a foothold in the ground could mature.

BISCHOFF, according to BUCHTIEN (1), reported finding monoecious gametophytes of *E. sylvaticum* bearing archegonia on their older parts and antheridia on the younger parts, and stated that monoecious gametophytes are not so rare as commonly believed. He found them occasionally in all his cultures. He also found the gametophytes of *E. sylvaticum* to be largely male, but many bore archegonia, and among these a comparatively large percentage bore antheridia also. He considered that the antheridia were formed after archegonia ceased to develop, but some bore them on different parts of the spreading meristem at the same time.

KASHYAP (**7, 8**), however, describes for *E. debile* much the condition found in these gametophytes of *E. laevigatum*, except that he rarely found antheridia occurring on gametophytes bearing sporophytes. Evidently the gametophytes examined by BUCHTIEN and KASHYAP very closely resembled those of *E. laevigatum* under consideration.

Sex organs

Archegonia (figs. 8, 13, 14) were present in all stages of development and agree closely with those described by BUCHTIEN (1), SADEBECK (9), CAMPBELL (2), HOFMEISTER (5), GOEBEL (3), and others. The only point of disagreement as to the archegonia of *Equisetum* appears in connection with the neck canal cells. In *E. laevigatum* the condition does not seem uniform. In many cases there is evidently only one neck canal cell. In a few archegonia, however, the vertical division had occurred and given rise to the two characteristic boot-shaped cells. The archegonial initial appears at any point on the peripheral meristem, not always on the under side, but in all cases the archegonia are pushed to the upper surface by the growth of the meristem below (figs. 8, 14). Branches usually develop at each side of an archegonium (fig. 14), so that when mature it lies between two branches.

Antheridia in large numbers also were present in all stages. They showed but one type of development, that characteristic of eusporangiate ferns. In the examination of more than fifty gametophytes in paraffin sections, only half a dozen antheridia were found on the upright branches. These (fig. 18), however, were not at the tip of the branch, but showed definitely the same development as others, which were developed in the massive meristem at the periphery of the thallus (figs. 9, 12, 13, 15–17). It is interesting to note that BUCHTIEN (1) considers even the antheridia developing at the tips of branches to be of the eusporangiate type. He says it seems that the antheridia at the tip of a filament and those in a cell mass develop differently, but it is only an apparent difference. In a filament there are no suitable conditions for antheridial development, so three vertical walls cut out surrounding cells which take the place of a thallus mass. Then the real antheridial initial is not the end cell of the filament, but the tetrahedal cell surrounded

by the three cells. This cell divides transversely and forms an antheridium exactly as is the case in the antheridia produced in the tissue. This is an interesting interpretation of the development of antheridia at the tip of a slender branch. As no such antheridia were found in these wild gametophytes, however, it does not apply to this case. The antheridia open by the disorganization of the entire outer wall as previously mentioned. In *E. laevigatum*, as was found by KASHYAP (7) to be the case in *E. debile*, antheridia often occur between the upright branches in exactly the position characteristic for archegonia. Figs. 12, 15, 17, and 19 show the beginning of these branches between antheridia.

Embryo

Embryo sporophytes in all stages, from a few cells to those with the third shoot an inch long, were abundant in most of the collections. The development was entirely characteristic of that commonly described for the group (JEFFREY 6, and others) (figs. 9, 11, and text fig. 1). The number of leaves on the primary shoot varies from three to four, and on the second shoot from four to five. Fig. 14 shows a very young sporophyte at about the 16-cell stage. In fig. 17 and text fig. 2 the sporophyte is still larger, while in fig. 9 the sporophyte shows all the body regions well organized. Fig. 11, a section of the plant shown at the right in text fig. 1, shows the primary branch well developed, with its first whorl of four leaves at the base. Its root emerges from the ventral side of the thallus. In text fig. 1 (at the right) part of the periphery of the thallus was cut away at *A*, where the cut surface shows. At the left of the gametophyte to the right in text fig. 1 and at the right of fig. 11 is the second shoot with several whorls of leaves and with its root emerging below. In this specimen the leaves on the second shoot were four in a whorl, the same as on the first shoot. In fig. 11 the bud for a third shoot shows at *B*. In text fig. 1 the sporophytes also show four leaves on the first shoot. This, however, was not universally true, many showing but three leaves (figs. 4, 7, 10). The roots for these shoots were well developed and deeply buried in the soil. Plants transferred to pots in the greenhouse are still growing vigorously (March 1).

Culture method

In connection with the study of the wild gametophytes, spores were planted in flats in the greenhouse and studies of young gametophytes and their development are under way. For a number of years gametophytes of *E. arvense* have been grown with considerable success. Each year sporophytes have lived until the primary shoot was a couple of inches tall, and in some cases the secondary shoot has developed. Because of this the same culture method was tried with *E. laevigatum*. The method used was as follows. An ordinary greenhouse flat was filled with sifted soil, a mixture of loam and sand being used. The soil was then smoothed and pressed down until a firm hard surface was formed an inch or more below the top of the flat. This was then flooded with water and allowed to stand until the water sank into the soil. Just as the water sank to the top of the soil the spores were shaken from the cones on to the soil. This was done by tapping the cone hard enough to shake the spores from the sporangia. The flat was then covered with a piece of glass and set in a sunny room of the greenhouse. Usually no more water was needed until the gametophytes were 1 mm. or more in diameter. If, however, the flats became too dry, they were watered by holding them in a tank of water until the soil became wet from below. After the gametophytes were 1 mm. in diameter they were sprinkled with an ordinary garden sprinkler. No attempt was made to sterilize the soil, nor were any special methods of watering used.

Flats of *E. laevigatum* planted in this manner in the middle of June grew well and developed archegonia and antheridia until the first of September. During the writer's absence of two weeks the greenhouse attendants changed and the flats were permitted to dry up. All were killed except one flat, in which sifted cinders from a railroad track were used instead of the usual soil. This flat survived the drought, and during the middle of September was full of sporophytes. Slugs ate these off as fast as they grew, however, so that none reached a height of more than a few millimeters. The gametophytes continued to grow, however, and new sporophytes developed only to meet the same fate. As winter approached the growth became slower and new sex organs did not

appear. Many gametophytes died, while others continued a sluggish growth. They are still alive (March 1) and show some growth, although on the whole no increase in size is observable.

By this same method spores of *E. arvense*, *E. telmateia*, and *E. robustum* sent from western Oregon, and of *E. arvense* from Chicago were also grown. These spores were planted about a week after gathering, and all grew well. *E. arvense* and *E. telmateia* developed sporophytes freely, but *E. robustum* never developed sporophytes, although the thalli lived until September 1 and attained a diameter of nearly 1 cm. before they died.

The fact that these spores grew well led the writer to plan some experiments in order to test the vitality of spores. Cones were taken when so green that the spores would not leave the sporangia. The cones were crushed and sprinkled on the soil. Others were planted when the spores were just ripe. Still others were kept in the laboratory in an open box for nine days. The cones were so dry they could be pulverized between the fingers when they were planted. In all cases equally abundant germination was observed, but the older the spores the longer the period before germinaton took place. Spores from green cones produced gametophytes of two and three cells during the first twenty-four hours, while gametophytes from spores dried for nine days required a week or more to reach the same stage. After being started they also developed more slowly. This agrees with BUCHTIEN'S results. He found that after fifteen days germination decreased greatly, and after twenty-one days only about 1 per cent germinated, and the growth was much slower. Studies of these gametophytes and their development are in progress, and the results will be given in another paper.

Summary

The investigation of large numbers of gametophytes of *E. laevigatum* found growing in their native habitat yielded results which may be summarized as follows:

1. The gametophytes are all of one kind.

2. They consist of a flat circular disk 1–10 mm. in diameter bearing numerous upright green branches on their upper surface,

and surrounded by a band of meristem which continues the growth of the thallus and produces archegonia and antheridia.

3. The gametophytes are typically monoecious. All bear archegonia and many antheridia also. Antheridia and archegonia occur without order on the thalli and often within a few cells of each other and of sporophytes.

4. Antheridia and archegonia may continue to develop until one or more sporophytes have attained considerable size.

5. Antheridia all develop as is characteristic of eusporangiate ferns, whether in a massive tissue or on a slender branch.

6. Archegonia develop as is characteristic of the group.

7. Sporophyte development is in agreement with common descriptions. The leaves of the first shoot are three or four in number, of the second shoot four or five.

8. Gametophytes grow to maturity under simple methods of culture.

The writer is indebted to Professor CHARLES J. CHAMBERLAIN for his interest and helpful suggestions during the progress of these studies, and for spores for culture growth; also to Mr. C. T. WALKER for spores sent from western Oregon, to Professor T. J. FITZPATRICK for the identification of sporophytes and for the careful reading of manuscript and proof, and to Mr. GEORGE SWALE, without whose efficient care of the greenhouse and cultures the experiments could not have been carried out.

UNIVERSITY OF NEBRASKA
LINCOLN, NEB.

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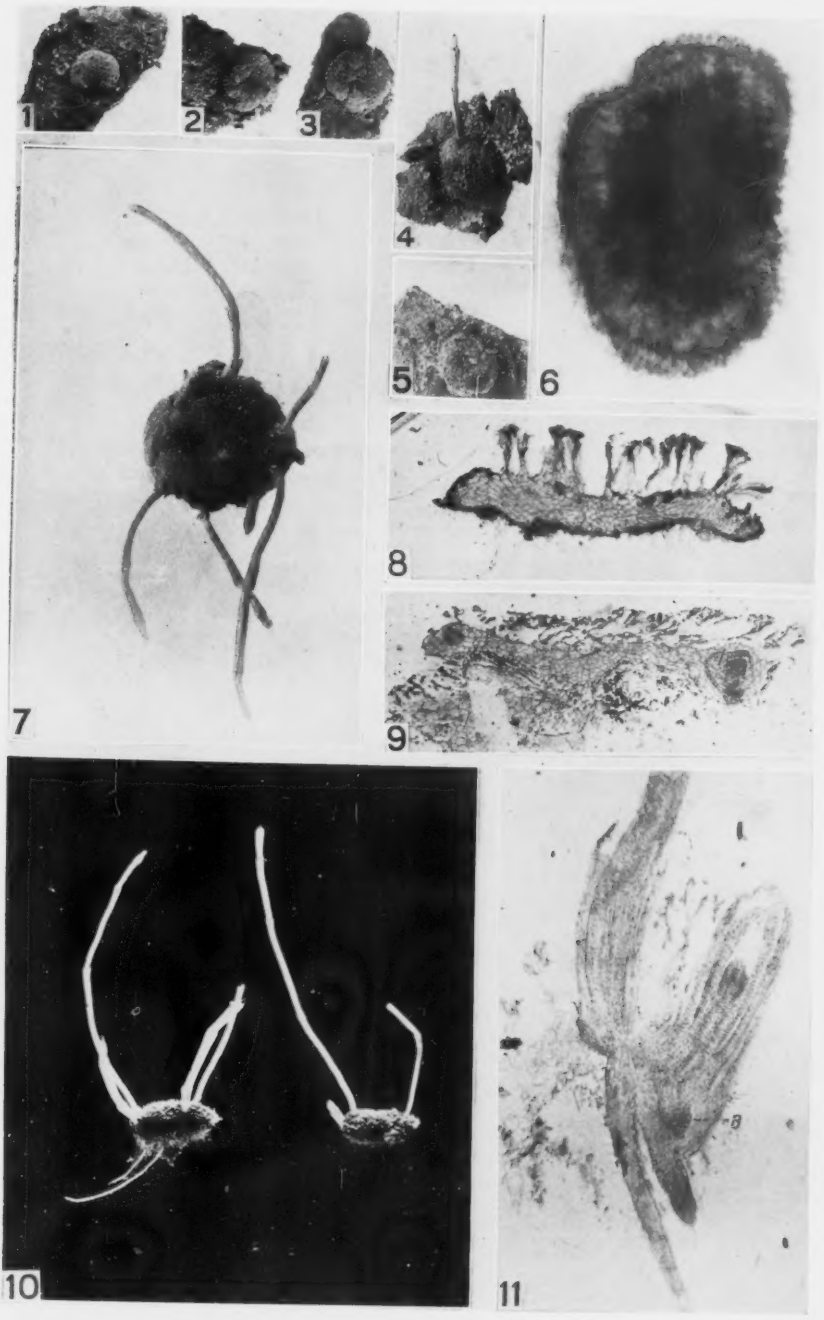
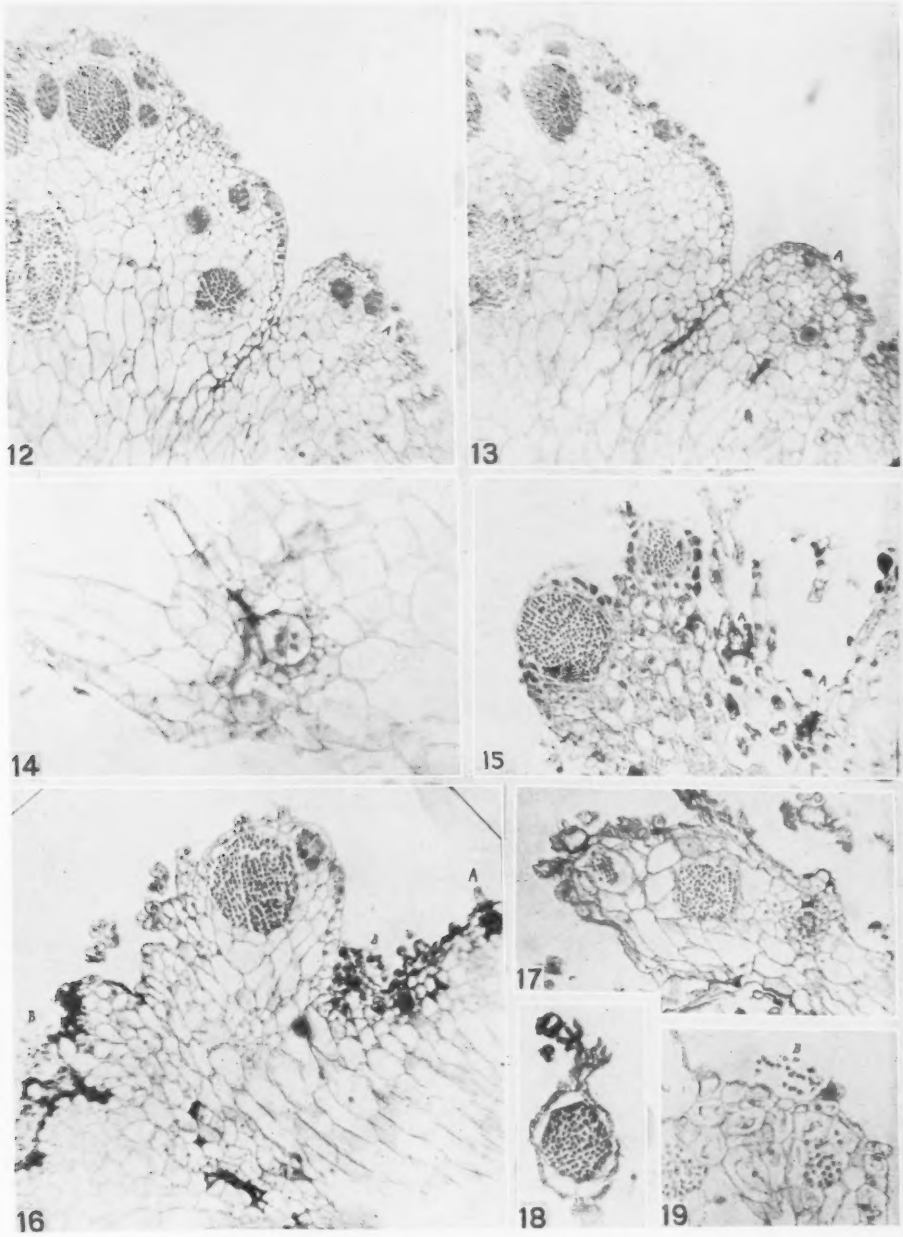


WALKER on EQUISETUM



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EXPLANATION OF PLATES XXIII, XXIV

PLATE XXIII

FIGS. 1–5.—Gametophytes attached to soil; ×2.

FIG. 6.—Under side of gametophyte in fig. 1 showing peripheral meristem, cleared in glycerine; ×11.

FIG. 7.—Gametophyte with five sporophytes at periphery; ×2.

FIG. 8.—Freehand vertical section of gametophyte showing massive parenchyma with upright branches and peripheral meristem bearing archegonia; ×12.

FIG. 9.—Vertical section of gametophyte showing two antheridia and one sporophyte; ×12.

FIG. 10.—Two gametophytes with soil removed (photographed under water); ×2.

FIG. 11.—Part of vertical section of gametophyte with sporophyte shown in text fig. 1 at right; ×18.

PLATE XXIV

FIGS. 12, 13.—Parts of horizontal section through peripheral meristem showing twelve antheridia and one archegonium; ×50.

FIG. 14.—Vertical section of archegonium with young sporophyte in venter; ×120.

FIG. 15.—Vertical section showing at left two antheridia; at right (*A*, *A*) necks of two old archegonia; ×50.

FIG. 16.—Horizontal section; above two antheridia intact; to their right and left (*B*) old ruptured antheridia; at extreme right (*A*) an old archegonium; ×50.

FIG. 17.—Vertical section showing two antheridia and archegonium containing young sporophyte; ×50.

FIG. 18.—Vertical section of upright branch with antheridium below tip; ×80.

FIG. 19.—Horizontal section; upper of three antheridia ruptured; ×60.

COMPARISON OF DEVELOPMENT IN DODDER AND MORNING GLORY[1]

GERTRUDE ELIZABETH MACPHERSON

(WITH PLATES XXV–XXVII)

The embryo of *Cuscuta Gronovii* Willd. is described in BRITTON and BROWN'S *Flora of the Northern United States and Canada* as follows: "Embryo linear, terete, curved or spiral, its apex bearing 1–4 minute scales; endosperm fleshy, cotyledons none." The purpose of this study was to determine whether there might not be at least a trace of cotyledonary development. In examining embryos of *Cuscuta*, which is a parasite, for indications of a rudimentary development of cotyledons, it seemed desirable to make a comparison with some non-parasitic species of the same family, and *Convolvulus sepium* L. was selected for this purpose.

By far the larger number of previous studies of *Cuscuta* have been concerned with the physiology of the plant, its host relationships, or geographical distribution, and few with the life history and morphology.[2] Miss HOOKER mentions the presence of scales on the inner and outer surface of the curve of the coiled embryo, but states that their position does not justify considering them cotyledons. The remainder of her paper discusses the habits of growth of *Cuscuta Gronovii*. COULTER and CHAMBERLAIN,[3] in discussing the endosperm, remark that, contrary to the usual course of development in parasites, the endosperm of *Cuscuta* is formed by free nuclear division, and later in treating of the types of embryos in Angiosperms they state that the embryo of *Cuscuta* is also an exception to the morphology of parasites in that it is large and well developed. These are the only important references to the embryo of *Cuscuta* that have come to the writer's attention.

[1] Paper no. 14 of the technical series, New Jersey Agricultural Experiment Station, department of plant pathology.

[2] HOOKER, HENRIETTA E., On *Cuscuta Gronovii*. BOT. GAZ. 14:31–37. 1899.

[3] COULTER, J. M., and CHAMBERLAIN, C. J., Morphology of angiosperms. Chicago. 1903 (pp. 174, 176).

The material was collected in September. The *Cuscuta* material was killed, part in a chromo-acetic solution and part in a picro-acetic solution, and the germinated seeds in a fixing solution consisting of 60 cc. of 95 per cent alcohol, 35 cc. of water, 5 cc. of formaldehyde, and 2 cc. of glacial acetic acid. All the *Convolvulus* material was killed in this latter fixing solution. The *Cuscuta* and *Convolvulus* were treated in the usual way and imbedded in paraffine, sectioned, and stained, some in haematoxylin, some in haematoxylin and eosin, and the larger part in iron-alum haematoxylin. The sections of *Cuscuta* were cut about 25 μ in thickness and those of *Convolvulus* about 10 μ in thickness.

The ovule in both species is anatropous (figs. 1, 20). The development of the embryo sac up to and including the 8-celled stage both for *Cuscuta* and *Convolvulus* follows the usual method. In the 2-celled stage of the embryo sac of *Cuscuta Gronovii* (fig. 2) there is a dense mass of protoplasm lying between and surrounding the two nuclei which are located at the ends of the sac. In the 4-celled stage (fig. 3) the sac is much larger and the protoplasm less dense. In the 8-celled stage (fig. 4) the sac is somewhat larger, and the protoplasm is most abundant immediately surrounding the polar nuclei. The synergids and egg are large, prominent, and somewhat irregular, but conform to the usual type. The antipodals are much smaller, but very distinct and well defined. The polars are oval, intermediate in size between those of the egg apparatus and the antipodals, and vacuolate. At this time the cells of the nucellus show the presence of a large quantity of starch grains (fig. 4), which, on account of their taking the stain so much more readily, render the nucellus very conspicuous. The cells of the nucellus are rich in starch, and those immediately surrounding the embryo sac show indications of rapid disintegration, accompanying the enlargement of the sac.

As previously stated, COULTER and CHAMBERLAIN describe the endosperm of *Cuscuta* as arising by free nuclear divisions and not by continuation of the process of cell division, with the formation of walls. This is contrary to the usual course of development of the endosperm in saprophytic and parasitic dicotyledonous

species. In most saprophytic and parasitic dicotyledonous plants the first division of the endosperm nucleus is accompanied by the formation of a wall which divides the sac into two chambers; but this is not true in *Cuscuta Gronovii*. The endosperm at all times is rather scanty, and this is especially true in the mature seed. The cells of the endosperm are elongated, with more or less elliptical nuclei, and are most frequently seen clustered around the embryo, rather than lining the sac as in *Piper medium*, *Potomageton* sp., etc. (figs. 18, 19).

The youngest embryo observed in *Cuscuta* was a 2-celled stage (fig. 5). It was spherical, and the basal cell was larger than the apical cell, both cells showing large, well defined nuclei. The two cells were evidently formed by transverse division of the fertilized egg. The later stages (figs. 5–7) appear to be the result of division in a number of planes and in no fixed order, resulting in embryos of irregular forms. The most usual form is an elongated type with a swollen base (fig. 8), having a suspensor of one cell, or no suspensor. There is a spherical type (figs. 9, 10) which is much less common. In later stages of development both spherical and elongated forms are found, in some cases with a 2-celled suspensor (figs. 11, 12), but more often with none. In neither spherical nor elongated forms is there any differentiation into dermatogen, nor later is there any indication of plerome or periblem. In some of the embryos where the shape is rather urnlike, the swollen base is formed by lateral enlargements (figs. 13, 14), but these cannot be an indication of cotyledons, for the cells of which they are formed are not differentiated in any manner from the rest of the embryonic tissue. Both the spherical and urnlike embryos continue to elongate (fig. 15) without any trace of differentiation, and finally form a long coiled embryo (fig. 16), large and well developed, and consisting of about two spirals, lying in the rather scant endosperm of the mature seed. The embryo of the mature seed bears two small scales near the apex (fig. 17*a* and *b*), one on the inner surface of the coil and the other slightly below this on the outer surface. Neither of these scales, however, from their relation to the other parts of the embryo, can be considered as cotyledons.

The stages in the embryo sac of *Convolvulus* are virtually the same, but smaller than in *Cuscuta Gronovii* (fig. 21). In the 8-celled stage the protoplasm is more dense than that occupying a similar position in the 8-celled sac of *Cuscuta Gronovii*. The synergids and egg do not differ much in size as in *Cuscuta*. The polar nuclei and antipodals are of similar appearance, but the polar nuclei usually stand out more prominently than the other nuclei. Here also the nucellar cells show evidence of degenerating rapidly. Starch grains are present in these cells, but not in the quantities in which they are found in *Cuscuta*.

The difference in the position of the nuclei in the sac is the most noticeable feature. In *Cuscuta* the nuclei extend from one end of the sac to the other, with protoplasmic connections between, while in *Convolvulus* the nuclei are gathered nearer the micropylar end of the sac, where the protoplasm is aggregated. The first division of the fertilized egg in *Convolvulus sepium* was transverse (figs. 22*b*, 23), and resulted in the formation of an embryo very similar to that of *Cuscuta Gronovii*. The 4- and 8-celled stages (figs. 24, 25) were elongated and somewhat irregular in form, and much the same as in *Cuscuta*, but never exhibited the pronounced urnlike form. In stages of more than eight cells the embryo of *Convolvulus* is spherical (figs. 27, 29) in form, with a rather pronounced dermatogen in the majority of cases (figs. 28, 29). The embryo continues its growth until in the mature seed it appears surrounded by scant endosperm, the two large cotyledons folded around the hypocotyl (fig. 30). No stages of the embryo intermediate between those of the period of development of fig. 29 and the mature seeds were studied, but these indicate that the differentiation into tissues must have been in accord with the stages of normal embryonic development. In these advanced stages there is a very large suspensor (fig. 27) consisting of large, very vacuolated, uninucleate cells, which completely fill the micropylar end of the sac and force the embryo well out into the sac. The enormous development of the suspensor is much more rapid than that of the rest of the embryo, from which its separation is not always definite. There is also more endosperm than in the corresponding stage of *Cuscuta*. The endosperm forms

more of a lining for the sac than in *Cuscuta*, and is also associated with abundant perisperm in a number of cases (figs. 26, 31). The entrance of the pollen tube through the micropyle can easily be traced in *Convolvulus*, although it is not apparent in *Cuscuta*. The pollen tube remains in *Convolvulus* (fig. 32*a* and *b*) as late as the 4-celled stage of the embryo or later, apparently without being ruptured. The actual fusion of the tube and egg nucleus was not observed.

One of the striking points about the embryo of *Convolvulus* is the frequent occurrence of polyembryony. In *Cuscuta* not one case was observed, but in *Convolvulus* it soon became evident that polyembryony was not the exception to the rule, but a usual occurrence in the development of the embryo. Polyembryony may be observed from the earliest stages until quite a highly developed embryo is present. In one case several embryos were lying in the micropylar end of the sac, two of them consisting of two cells with a 1-celled embryo also present (fig. 22*a* and *b*), and 8-celled stages with one or more 1- or 2-celled embryos present were frequently observed (fig. 25), as were larger embryos that had the dermatogen developed (fig. 26). These extra embryos never developed at the antipodal end of the sac, and do not appear to be formed by the budding off from the fertilized egg. They seem rather to be formed from the synergids, or it may be that some of what appear to be 1-celled embryos are rather persistent synergids that have not developed any further and have not been absorbed. There may be some basis for assuming that polyembryony is the result of parthenogenesis.

Summary

1. Except for the enlargements of undifferentiated tissue on the sides of some of the embryos of *Cuscuta*, there appears to be no cotyledonary development.

2. The development of a large vacuolate suspensor is typical of the older embryos of *Convolvulus*.

3. Polyembryony is the rule rather than the exception in the development of the embryos of *Convolvulus*.

4. Multiple embryos in *Convolvulus* seem to be developed from the synergids.

5. The endosperm in *Cuscuta* is scanty, and in both *Convolvulus* and *Cuscuta* is the result of free nuclear division.

The writer wishes to thank Dr. MEL. T. COOK for suggesting this problem, and for his interest and assistance throughout the course of the investigation.

RUTGERS COLLEGE
NEW BRUNSWICK, N.J.

EXPLANATION OF PLATES XXV-XXVII

PLATE XXV

FIG. 1.—Longitudinal section of flower of *Cuscuta Gronovii*, showing position of ovule.

FIG. 2.—Longitudinal section of *Cuscuta Gronovii*, showing 2-nucleate stage of embryo sac.

FIG. 3.—Four-nucleate stage of embryo sac.

FIG. 4.—Eight-nucleate stage of embryo sac before mature organization, showing degenerating cells of nucellus, rendered prominent by presence of large number of starch grains.

FIG. 5.—Two-celled embryo.

FIG. 6.—Four-celled embryo with suspensor.

FIG. 7.—Eight-celled embryo, elongated type with swollen base.

FIG. 8.—Older embryos, same type as fig. 7.

FIG. 9.—Embryo of more spherical type.

FIG. 10.—Advanced embryo of elongated form.

FIG. 11.—Advanced embryo of spherical form with 2-celled suspensor.

FIG. 12.—Same type of embryo as fig. 11.

PLATE XXVI

FIG. 13.—Advanced embryo of urnlike form.

FIG. 14.—Urnlike embryo slightly older than fig. 13.

FIG. 15.—Very advanced embryo, showing elongation not accompanied by differentiation of embryonic tissue.

FIG. 16.—Coiled embryo as found in mature seed.

FIG. 17.—Apex of embryo showing two scales (*a*); apex of embryo showing structure of scale (*b*).

FIG. 18.—Endosperm in *Cuscuta* surrounding embryo rather closely.

FIG. 19.—Perisperm sometimes seen accompanying endosperm in *Cuscuta*.

FIG. 20.—Longitudinal section of *Convolvulus sepium*, showing type of ovule.

FIG. 21.—Eight-nucleate stage of embryo sac.

PLATE XXVII

FIG. 22.—Sac showing polyembryonic condition, containing 1- and 2-celled embryos (*a*); 1- and 2-celled embryos (*b*).

FIG. 23.—Two-celled embryo.

FIG. 24.—Four-celled embryo.

FIG. 25.—Older embryo and smaller one.

FIG. 26.—Older embryo with several 1- and 2-celled embryos, accompanied by abundant perisperm.

FIG. 27.—Young spherical embryo with suspensor of many vacuolate cells.

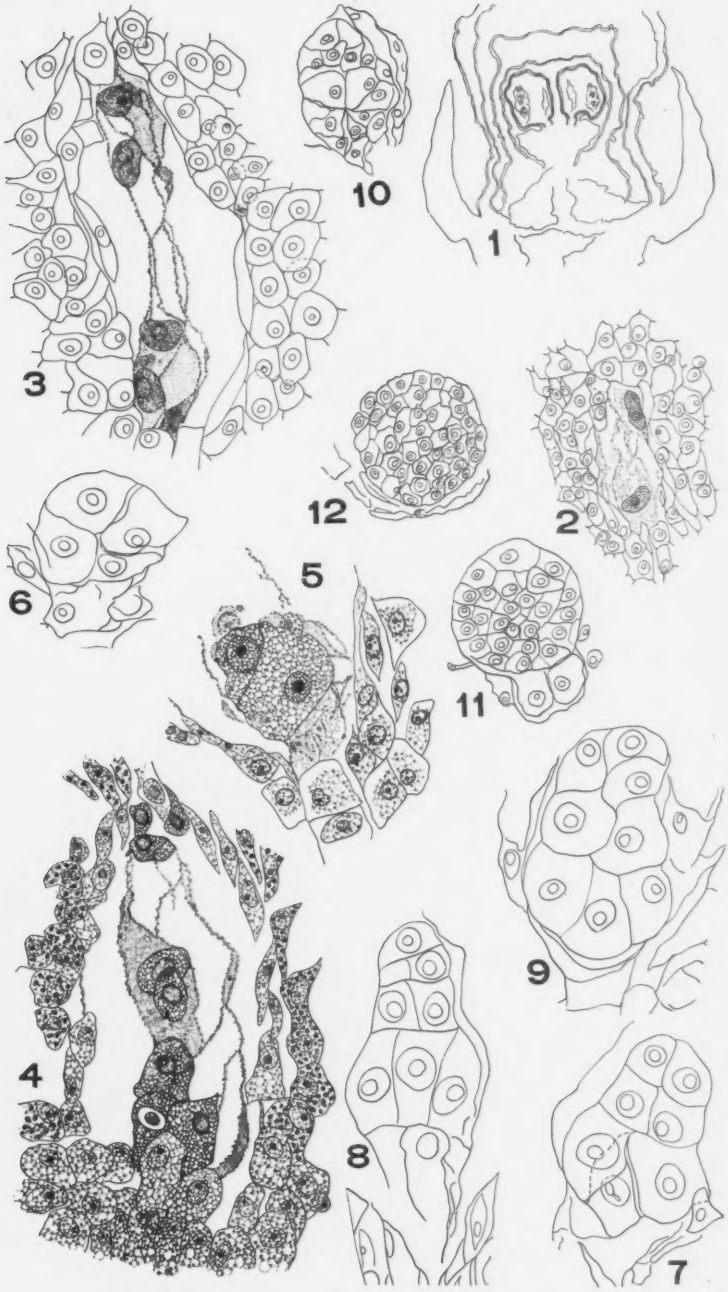
FIG. 28.—Older embryo and suspensor.

FIG. 29.—Advanced embryo of spherical type.

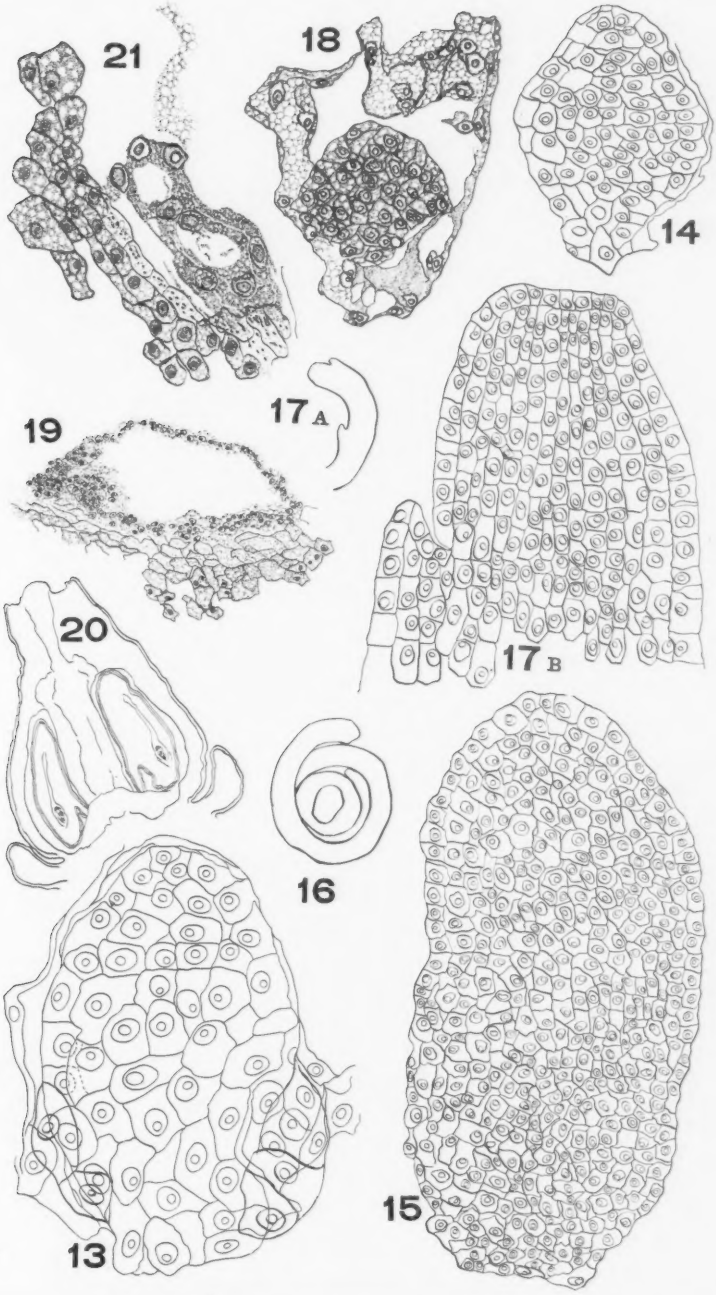
FIG. 30.—Embryo as found in mature seed, showing cotyledons and hypocotyl.

FIG. 31.—Endosperm in *Convolvulus* lying next to nucellus rather than close to embryo.

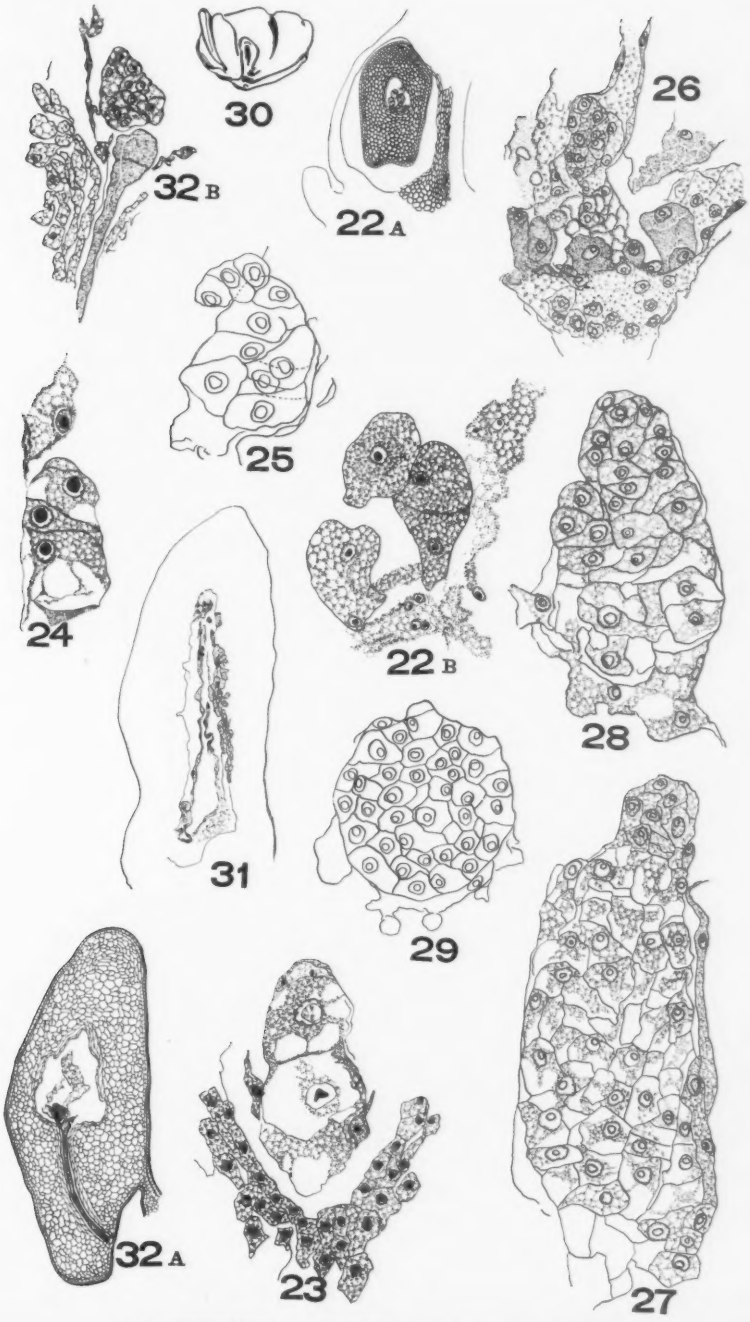
FIG. 32.—Sac containing many-celled embryo, showing entrance of pollen tube and inflated tip, with no indications of rupturing (*a*); same view showing micropylar end of sac (*b*).



MACPHERSON on CUSCUTA and CONVOLVULUS



MACPHERSON on CUSCUTA and CONVOLVULUS



MACPHERSON on CUSCUTA and CONVOLVULUS

BRIEFER ARTICLES

SIMPLE DEVICE FOR WEIGHING SEEDS

(WITH ONE FIGURE)

In biological work it is often necessary to determine the weight of individual seeds. The use of the usual analytical balance is too slow if large quantities are to be weighed, and the spiral spring balances are often not delicate enough to weigh small seeds.

A glass scale can be made in a short time which is accurate and permits rapid work. A piece of glass tubing is heated over a Bunsen burner and drawn into a long rod. The rod should be about 1 or 1.5

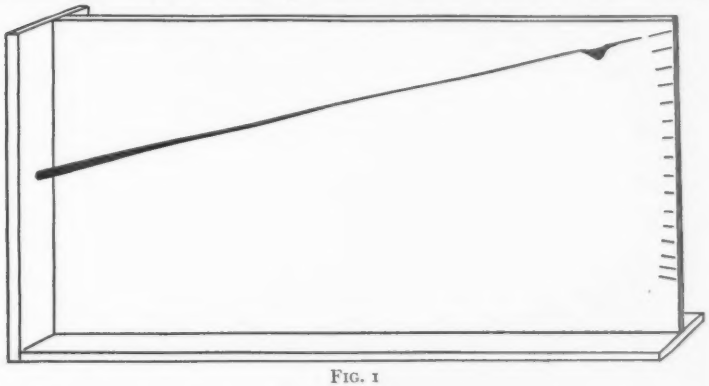


FIG. 1

mm. thick and 50 cm. long for weighing seeds of corn or beans. The tip of the rod should be bent and a paper tray glued on. A bristle or piece of fine wire attached to the tray serves as a pointer. The base of the rod is inserted in a hole bored in the upright base board. The scale is graduated by using the weights for the analytical balance (fig. 1). The writer has two scales on the same stand, one for beans and corn which is accurate to one centigram, and one for wheat and oats which is fairly accurate to one miligram.

If the forefinger of the left hand is placed under the tray while placing the grains on with a pair of forceps the pointer will come to rest almost immediately. With a little practice 300–400 seeds can be weighed per hour. Constant use for several weeks at a time does not seem to cause any loss in elasticity of the glass rod, but the scale should be checked occasionally.—KARL SAX, *Maine Agricultural Experiment Station, Orono, Maine.*

USE OF CHLOROIODIDE OF ZINC IN PLANT HISTOLOGY

Chloroiodide of zinc has fallen more or less into disuse in the botanical laboratory, perhaps because of its apparent vicissitudes. Since it is unequaled in usefulness in histological work, however, it is advantageous to workers who still believe in the practicability of the old-fashioned hand-section razor to obtain a working knowledge of this reagent.

By the use of the "one solution" mixture (Behrens: 25g $ZnCl_2$, 8g KI, 1.5g I, 8cc water) negative results are often obtained, but when properly prepared and kept from deterioration, the solution may be used for a number of years. To insure uniform results, the two solution mixture, first suggested by NOVOPOKROWSKY, is recommended. Solution *A*, iodine potassium iodide 1:1:100; solution *B*, zinc chloride 2 parts, water 1 part. Stain in solution *A* for a few seconds and then transfer to solution *B*. Keep object moving in a drop of this second solution until a bright blue color is obtained. To hasten the reaction and to intensify the color it sometimes becomes necessary to add a drop of solution *A* subsequent to the treatment with solution *B*. The rapidity of the staining and the intensity of the color obtained often depend on the nature of the membrane. Certain tissues will stain only after prolonged treatment, but most herbaceous material will react very readily.

Since iodine dissolves in water very slowly, it becomes necessary to prepare the reagent some time before it is desired for use. When a section of a potato stem is stained by this method, for example, and the preparation viewed under the microscope, it is seen that the cellulose membranes are a bright blue, lignified, cutinized, and suberized walls a yellowish brown. Young phloem fibers and immature xylem cells, of course, take the cellulose stain. The staining reaction of the sieve tubes of the primary phloem groups is most striking in cross-sections. Their intenser stain and the heavier walls stand out conspicuously in contrast with the phloem parenchyma cells, which stain like ordinary parenchyma of pith or cortex. The pathological anatomist finds the chloroiodide of zinc especially useful in the study of necrotic tissues, since the double staining obtained by this method permits of a more searching inquiry into the nature of the cell wall changes than is possible with a one-sided differential stain like the classic phloroglucin-HCl reagent. The use of the chloroiodide of zinc stain may occasionally call for some patience, but the results obtained warrant and reward it in every case.—ERNST ARTSCHWAGER, *Cornell University*.

CURRENT LITERATURE

BOOK REVIEWS

Bacterial diseases of plants

This volume by SMITH,[1] as its name indicates, is intended to serve students as an introduction to that group of plant diseases caused by bacteria. An unusual proportion of the text is based upon the work of the author and those associated with him in his laboratories. The wealth of illustration, including reproductions of photographs and drawings, is particularly striking. There are 237 full-page illustrations, and smaller illustrations bring the total to about half of the book.

The first 64 pages are devoted to "A conspectus of bacterial diseases of plants," including tables of plant families and genera in which bacterial diseases are known. Of particular interest are the summaries of agents of transmission and on plant reactions. "Methods of research" are discussed in about 50 pages. In most cases details of culture media and technique are omitted, reference being made to suitable sources of information.

Part III, the principal portion of the text, is devoted to a "Synopsis of selected diseases." Of the fourteen organisms discussed, eight were named by the author, and two others by workers in his laboratory, and all have been worked over by him or his associates, so that statements are in general authoritative. The diseases and causal organisms discussed are those which have been most studied in the United States. For each disease there is given, first, a brief description of the pathology, plants affected, and distribution; second, a condensed description of the causal organism, including morphology, staining characters, culture, and physiology; and third, the special technique required in studying the relationships of parasite and host. In each instance this is followed by a laboratory guide, indicating the points to be studied and the special observations to be made. A brief index to the more important literature is included. The directions are full of suggestions for experimentation and the development of original problems.

The next 100 pages are included in a section termed "Miscellaneous." Brief notes on additional diseases are followed by a chapter on suggestions of subjects for special study. The next three chapters are devoted to tumors and teratoses produced in plants in the absence of parasites. They are of great interest, but would seem to belong rather to a treatise on general plant pathology than in one devoted to bacterial diseases.

[1] SMITH, ERWIN F., An introduction to bacterial diseases of plants. pp. xxx+688. *figs.* 453. Philadelphia: Saunders Co. 1920.

The last section on "General observations" is unique. It consists of about 30 pages of advice to students and investigators. It is well written, interesting, and stimulating. It is to be regretted that it should have been published where it will necessarily have relatively so small a circle of readers. The ideas running through the section may be indicated by some of the headings, as "On subsidiary studies," "On beginning work thoughtlessly," "On repetition of experiments, other people's, one's own," "On publication," "On keeping one's own counsel," "On sharing credits," and "On attending meetings and keeping up membership in societies, and on being generally public spirited and helpful in science." An excellent index is provided.—R. E. BUCHANAN.

Geography of plants

In a compact volume, HARDY[2] has given a comprehensive review of the vegetation of the world in very readable form. Maps of such climatic factors as rainfall and temperature, as well as of the vegetation itself, are upon a small scale, but seem very accurate, although necessarily lacking in detail and expressing a much greater rigidity than obtains in nature. The general characterization of the vegetation is fairly accurate, although one is often at a loss to know just what genera and species are intended on account of the rather complete absence of scientific names. The few scientific terms employed are so lacking in accuracy as to shake one's confidence in the facts presented with which he is not already familar. Irregularities in spelling and capitalization might be overlooked, but to designate the long-leaved pine on the Atlantic slope as *Pinus Lambertiana*, or to refer any of the North American "cedars" to the genus *Cedrus* is certainly unpardonable. Such inaccuracies in terminology, together with an entire absence of citations of the sources of data, will prevent the book being used by advanced classes, although it will probably be found useful for imparting general impressions and in sketching in broad outline the vegetation of the various continents.—GEO. D. FULLER.

MINOR NOTICES

Practical botany.—MARTIN'S textbook entitled *Botany for Agricultural Students* has appeared in a second edition and with a new title.[3] The general purpose of the text was stated in a previous review.[4] In the new edition portions of the text have been re-written, to correct errors and to increase clearness, but the chief changes occur in the treatment of heredity and evolution, a chapter on variation being added. The matter is well presented, clear in style and organization, and is certainly well adapted to its constituency.—J. M. C.

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[2] HARDY, M. E., The geography of plants. 12mo. pp. xix+327. *figs. 115*. Oxford: Clarendon Press. 1920.

[3] MARTIN, J. N., Botany with agricultural applications. 8vo. pp. xii+604. *figs. 490*. New York: Wiley & Sons. 1920.

[4] BOT. GAZ. **68**:308. 1919.

NOTES FOR STUDENTS

Ecological concepts and nomenclature.—All recent discussions of the classification of vegetation make it evident that ecologists are far from agreement upon any one system. The resulting ambiguity and confusion are deplored by both TANSLEY[5] and PAVILLARD.[6] The latter gives further emphasis to his former statement that the species and the association constitute the two fundamental unities of ecology or geobotany, and his two main divisions of the subject are based on these unities. As each of these units may be considered from the floristic, the genetic, and the ecological viewpoint, there results six subdivisions of the science. Considering the desirable implications of the term "phytosociology" when used to designate the study of plant communities, and translating PAVILLARD's terms freely, the six subdivisions of ecology may be designated: (1) floristic geobotany, (2) genetic geobotany, (3) ecologic geobotany, (4) floristic phytosociology, (5) genetic phytosociology, and (6) ecologic phytosociology. The first three are devoted to the consideration of the species and the others to the problems of the associations. Something of the content of the various subdivisions has been noted in a previous review.[7]

In the present article PAVILLARD devotes much attention to the considerations which would establish the association as the fundamental unit in the investigation of vegetation. With this TANSLEY seems in agreement, and further holds that such a unit of vegetation should correctly and usefully be regarded as an organic unity or quasi-organism. TANSLEY, however, would limit the application of the term "association" to mature units in relatively stable equilibrium with their environment. These are the climax associations or permanent associations of other ecologists. To transitory or developmental associations he would apply CLEMENTS' term of "associes."

Being in agreement that the association is the fundamental unit of phytosociology, TANSLEY and PAVILLARD emphasize the importance of the study of its development, the former clearly recognizing the principal of "succession" and the existence of both climatic and physiographic (edaphic) climaxes, and the latter devoting one of his subdivisions of the science ("genetic phytosociology") to problems of the development of associations, although he points out that such studies are not often undertaken or appreciated in continental Europe. TANSLEY insists upon the study of the morphology of associations, that they are essentially topographical units, and are in the first instance to be determined empirically, while PAVILLARD regards floristic composition as their most essential characteristic. This floristic composition includes not only accurate lists of the species, but also consideration of the

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[5] TANSLEY, A. G., The classification of vegetation and the concept of development. Jour. Ecol. 8:118–149. 1920.

[6] PAVILLARD, J., Espèces et associations; essai phytosociologique. Montpellier. pp. 34. Oct. 1920.

[7] BOT. GAZ. 70:183–185. 1920.

"sociological value of the species," and here perhaps lies the most valuable and suggestive portion of the French writer's contribution. He asserts that the "sociological value" of species depends upon their abundance, dominance, sociability, constancy, affiliation (fidélité), and genetic importance. When "abundance" and "dominance" are determined in a quantitative manner according to RAUNKIAER'S[8] methods, "constancy" according to DU RIETZ, affiliation according to BRAUN-BLANQUET, and "genetic importance" according to PAVILLARD, the results will greatly clarify our concept of the association and give a new importance to its floristic study. The "genetic coefficient" expressing the relative importance of the species in the development of the association is perhaps the most important of these concepts and represents a decided contribution from PAVILLARD.

While there is practical agreement as to the importance of associations and little difference as to the use of the term, these two writers fail to agree when it comes to the consideration of units of a higher order. TANSLEY holds that the "formation" corresponds to habitat and cannot be satisfactorily characterized by life forms. He applies the term "formation" to a set of plant communities related developmentally and culminating in one or more associations. On the contrary, PAVILLARD regards life form as the only characteristic of a "formation," which may thus be a community that is but a fragment of an association or one that contains several associations. He does not think that a satisfactory system of classification of plant associations is practicable in the present state of our knowledge.

In attempting, in his admirable discussion, to harmonize the widely divergent opinions and the diverse attitudes of different ecologists, TANSLEY has been the first, perhaps, to appreciate fully the influence not only of difference of training and of centers of interest but also of geographical situation. To himself it is not surprising that American ecologists, with their abundance of entirely natural areas, should belong to a school favoring a system based upon climatic climaxes and succession, or that those located in the middle west or northeast of the United States should appreciate the importance of edaphic factors and distinguish their action from those of climatic origin.

A similar consideration of the influence of geographical situation would probably have been useful to ROMELL[9] in explaining the segregation of Swiss and Scandinavian ecologists in the "inductionist" school, and the American and English scientists in the "successionist" school. He shows, however, that some of the former, notably SERNANDER, have appreciated the dynamics of vegetation and employed many of the methods of the latter. His plea for the use of hypotheses and of experimental methods is excellent, and the

[8] RAUNKIAER, C., Recherches statistiques sur les formations végétales. Det. Kgl. Danske Videirkabernes Selskabe Biol. Meddeleser I. **3**: pp. 80. 1918.

[9] ROMELL, LARS-GUNNAR, Physionomistique et écologie raisonnée. Svensk Bot. Tidsk. **14**:136–146. 1920.

reviewer is ready to agree with his conclusion that "the watchwords of a rational and reasonable ecology are logic, common sense, and physiological experimentation," and perhaps to echo his "We do not need their dogmatism nor their abominable nomenclature; we have enough of our own."—GEO. D. FULLER.

Alpine adaptations.—In 1884 BONNIER began his classical experiments upon the structural changes induced by growing plants at various altitudes. Plantations were made in the lowlands and at various altitudes in the Alps, so arranged that the two individuals to be compared were produced by dividing one plant. Similar experiments were begun in the Pyrenees in 1886, and the botanical world is familiar with the remarkable results as reported in BONNIER'S earlier publications. Now after a lapse of over 30 years he makes a summary of what are probably the most notable and prolonged experiments of their kind on record.[10]

A few of the plants taken from the plains to alpine stations died, but a list is given of 58 species that proved able to maintain themselves at high altitudes. These have all undergone changes which make them closely resemble indigenous alpine plants. The principal changes are relatively large development of the subterranean as compared with aerial parts, shortening of the leaves and of the internodes of stems, increased hairiness, and relatively larger development of bark and protective tissue. The leaves became thicker in proportion to their surface and are a deeper green, with more highly developed palisade tissue and a larger number of chloroplasts, while the flowers are larger and more highly colored. In at least 17 species the changes are so great that the plants have apparently been transformed into distinct alpine "species." Thus *Lotus corniculatus* L. began to show decided modifications within 10 years, and finally became identical with *L. alpinus* Schleich; *Helianthemum vulgare* Gaertn. has in 30 years become *H. grandiflorum* DC.; while *Leontodon proteiformis* Vill. in 6 years is completely transformed into *L. alpinum* Vill.

For all the species able to maintain themselves with considerable altitudinal range, there seems to be an optimum altitude at which the transformations are most rapid, most complete, and where intensity of color and development of chlorenchyma reach a climax. Species of *Potentilla* may be cited as indicating individual differences of range. Thus the optimum conditions for *P. argentea* appear to be found at 1050 m., for *P. reptans* at 1500 m., and for *P. tormentilla* at about 2000 m. Cultures of alpine plants at lower altitudes showed reversed although less marked transformations. Alpine species, able to maintain themselves at various altitudes, at the lower stations gradually lost many of their typically alpine characteristics, and a list of 14 species showing such changes is given. Certain annuals taken from the

[10] BONNIER, GASTON, Nouvelles observations sur les cultures expérimentales à diverses altitudes et cultures par semis. Rev. Gén. Bot. 32:305–326. *pls 2. figs. 4.* 1920.

plains and transplanted to high altitudes became biennials or perennials, as *Poa annua* and *Senecio viscosus*, while *Calamintha acinos* became not only perennial but subfruticose.

In 1919 seeds from known individuals were sown on July 1 at Fontainebleau at an altitude of 78 m., and in the Pyrenees at 2000 m. The resulting plants were compared on September 30, and all at the alpine station showed decided dwarfing. In spite of the fact that many species did not reach maturity in the mountains, several showed the mature form of leaf earlier than in the lowland. Some species, such as *Sinapis arvensis* and *Centaurea cyanus*, proved by their flowering that the dwarfed alpine individuals were quite mature. Many of the alpine forms exhibited a decidedly increased development of hairs and of anthocyan.—GEO. D. FULLER.

Lycopodium.—HOLLOWAY,[11] in his fourth paper on New Zealand species of *Lycopodium*, presents sections PHLEGMARIA and CERNUA, the former represented by *L. Billardieri*, with its var. *gracile*, and *L. varium*, the latter by *L. cernuum*, *L. laterale*, and *L. ramulosum*.

In the PHLEGMARIA group the general form of the prothallium "consists essentially of a central body of tissue which may be either bulky or more or less elongated, and a number of branches which arise adventitiously from the central body." The plants are dorsiventral and the sex organs zonate. The latter arise "immediately behind the apex" of either the main body or the branches, and are associated with numerous paraphyses. The archegonia occur only on the central body. The endophytic fungus may occupy the entire mass of cells of the main body when young, except the generative tip and the epidermis. In the older plants there is a central layer of elongated cells free from the fungus, probably functioning as "translocation tissue." The identity of the fungus has not been settled, but HOLLOWAY has shown the sporelike bodies observed by other investigators. His figures of the fungus in *L. Billardieri* show exactly the habit of the fungus in the prothallia of *L. lucidulum* observed by the reviewer. The same thing is probably to be found in the prothallium of *L. Selago*. The relationship of the four embryonic organs is well shown in fig. 34.

There is an excellent discussion of body form, comparing prothallia of this section with those of the *Selago* group. HOLLOWAY states that the *Phlegmaria* type of prothallia is "the extreme attained by the cylindrical type of growth"; and that the *clavatum* type is "the extreme attained by the continued conelike manner of growth."

In considering the representatives of CERNUA, most attention is given to *L. ramulosum*. It is an interesting fact that chlorophyll never occurs in the lower part of the prothallium. The fungus is limited to shallow zones, is

[11] HOLLOWAY, Rev. J. E., Studies in the New Zealand species of the genus *Lycopodium*. IV. Trans. New Zealand Inst. 52:193–239. 1920.

epidermal, and both intercellular and intracellular. In the protocorm "it seems to be always present in an intercellular position in the central tissues." The demonstration of the fungus in this structure inclines the author toward "BOWER's suggestion" concerning the phylogenetic importance of the protocorm. The most interesting thing to the reviewer is HOLLOWAY's discovery that the germinating spore sometimes develops a filament before the "primary tubercle" stage of TREUB is reached. This fact throws some light upon the phylogenetic history of the *Lycopodium* prothallium.

In a discussion of the cause of such a variety of form in the prothallia of *Lycopodium* and *Tmesipteris*, the author says "One cannot avoid the suggestion that the dominating factor . . . . is the presence of the fungus." He suggests that the primary tubercle may be a secondary growth rather than a primary one.—E. A. SPESSARD.

Wilting coefficient studies.—Considerable surprise was expressed at the announcement by BRIGGS and SHANTZ of the "wilting coefficient" as an important critical factor in the relation of soil moisture to the plant, and at their statement that the wilting coefficient was practically the same for all classes of plants and showed little or no variation in response to atmospheric changes. Many seemed to doubt the accuracy of these statements, and several unsuccessful attempts were made to demonstrate a relationship between the evaporating power of the air and the wilting coefficient. SHULL[12] showed rather conclusively that the wilting coefficient is a function of the movement of water in the soil rather than a lack of gradient of forces tending to move the water toward the plant. As a function of the soil finding an expression through plants, rather than a function of the relationship of the forces exerted by the plant, it does not seem surprising that the wilting coefficient is much the same for all plants and for all atmospheric conditions.

Attacking the problem from a somewhat different angle, LIVINGSTON and KOKETSU[13] show even more conclusively that the wilting coefficient is a function of water movement in the soil. These workers made use of small porous porcelain cones or "soil-points" which, while dry, were thrust into the soil. At the end of a suitable period they were withdrawn, and by weighing the amount of water absorption was determined. The data obtained indicated that at permanent wilting the water supplying power of the soil was the same for the different plants used and also for different soils within certain limits. They regard this present report a tentative and preliminary one, but in the soil-point method there seems to be much promise of a complement to the porous cup atmometer investigations of the moisture conditions of the atmosphere.—GEO. D. FULLER.

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[12] SHULL, C. A., Measurement of the surface forces in soils. BOT. GAZ. **62**:1–29. *figs. 5.* 1916.

[13] LIVINGSTON, B. E., and KOKETSU, R., The water supplying power of the soil as elated to the wilting of plants. Soil Science **9**:469–485. 1920.

Studies of cambium.—BAILEY,[14] in continuation of his studies of cambium, has considered the size variations of cambial initials in Gymnosperms and Angiosperms, making an extensive reconnaissance through the representatives of these groups, tabulating measurements of 13 species of Gymnosperms and 54 species of Dicotyledons. He finds striking variations in the dimensions of the cells of the cambium and secondary xylem, some of the variations being purely somatic, while others are germinal. He finds that in many plants the dimensions of tracheary cells are determined by those of the cambium initials, while in other plants the dimensions are due to changes during the differentiation of the xylem. He concludes that these fundamental types of size variations and the fluctuations in form and structure are significant in the investigation of certain cytological, morphological, and physiological problems. He calls attention to the fact that the cambium is an unusually favorable medium for the study of problems relating to cell size and body size, the working sphere of the nucleus, the nucleocytoplasmic relation, and phenomena of cytokinesis in somatic tissues.—J. M. C.

Morphology of Larix.—In a study of various stages in the life history of *Larix leptolepis*, Doyle[15] brings out some points of interest. His study of the cavities at the apex of the microsporophyll leads him to conclude that they are homologous with similar cavities in the vegetative leaves, and that they do not represent abortive sporangia. He also suggests that similar cavities in *Ginkgo*, *Torreya*, and other forms may have as little relation to a previous spore-producing function. The microspore, which is wingless, is shed with the stalk and body cells already formed, as in *Abies*. Some of the figures would indicate that the nuclear membrane in the stalk and body cells had been overlooked and only the nucleolus recorded. The amount of variation and the number of peculiar conditions are about what one might anticipate in a thorough study of almost any Gymnosperm. In the ovulate cone there is a gradual transition from vegetative leaves to cone bracts, as in *Pseudotsuga*. The general conclusion is that numerous similarities indicate a distinct natural affinity between *Larix* and *Pseudotsuga*.—C. J. CHAMBERLAIN.

North American Flora.—Parts 5 and 6 of volume 7 include a continuation of Aecidiaceae by ARTHUR and his colleagues, chiefly the genus *Dicaeoma*, under which 269 species are recognized. The following genera are also included: *Pucciniola* (25 spp.), *Allodus* (49 spp.), and *Klebahnia* (8 spp.).—J. M. C.

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[14] BAILEY, I. W., The cambium and its derivative tissues. II. Size variations of cambial initials in Gymnosperms and Angiosperms. Amer. Jour. Bot. **7**:355–367. *figs. 3.* 1920.

[15] DOYLE, J. D., Observations on the morphology of *Larix leptolepis*. Sci. Proc. Roy. Dublin Soc. **15**:310–330. *pls. 17, 18.* 1918.

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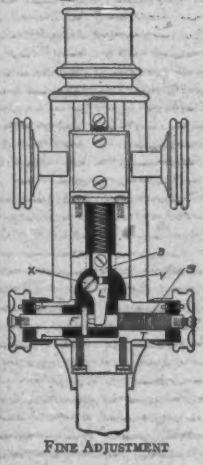

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